INVASIVE SPECIES, SPATIAL ECOLOGY, AND HUMAN-WILDLIFE CONFLICT: EXPLORATION OF WILDLIFE SCIENCES IN THE PRESENT

By

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ABSTRACT

INVASIVE SPECIES, SPATIAL ECOLOGY, AND HUMAN-WILDLIFE CONFLICT: EXPLORATION OF WILDLIFE SCIENCES IN THE PRESENT

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Wildlife sciences are continually shifting in response to global environmental change, arising threats to conservation and the sustainability of natural resources, and technological and analytical advances. As such, wildlife professionals are required to have a diverse skillset for addressing these challenges. My dissertation focuses on a variety of topics that are currently at the forefront of interest and in the purview of wildlife sciences moving forward. In Chapter 1, I describe various behaviors and spatial ecology of a widely distributed and detrimental invasive species in North America ─ the wild pig. I collated global information from published research on wild pigs to describe the ecology of this species and identify areas that merit additional research. In Chapter 2, I explore capacity of wild pigs to act as exotic engineers and quantify their impacts to biotic and abiotic properties in Michigan. I found wild pigs to adversely influence diversity of plants of high conservation value, and reduce concentrations of macronutrients and ammonium in soils, having implications for how this species functions in northern systems. In Chapter 3, I explored wild pig movement and activity in Michigan. Previously, limited information existed on movements and activity of wild pigs in northern systems, and this research provides a foundation for understanding wild pig movement ecology in these newly colonized regions. In Chapter 4, I assessed the spatio-temporal signatures of lion roaring in relation to a dominance shift in Addo Elephant National Park. I found that subordinate males roared less and constrained roaring to the interior of their range, likely to lower chances of

being overheard by the dominant male coalition. In Chapter 5, I examined the research-implementation gap pertaining to human-carnivore conflict (HCC) research being conducted in East Africa. I found evidence that current HCC research lacks evidence of interdisciplinarity and seldom included practitioners. In addition, studies rarely engaged local stakeholders in the research process or explicitly listed management and conservation actions as objectives. The breadth of my research displays a diversity of techniques, subject matter, and topics currently at the leading edge of wildlife science. Results of this research provide contributions to invasive species management, wildlife conservation, behavioral ecology, as well as development and practice of conservation research.

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PREFACE

Each chapter within this dissertation was originally drafted as a standalone manuscript for publication in a peer-reviewed journal. Chapter 1 is currently in press to be included in a book titled *Invasive Wild Pigs in North America: Ecology, Impacts, and Management*, published by CRC Press, Taylor & Francis Group, Boca Raton, Florida. Chapter 2 is in review at *Journal of Wildlife Management*. Chapter 3 has not been submitted, and Chapter 4 was submitted and accepted for publication in the *Journal of Mammalogy*. Chapter 5 is in review in *Animal Conservation*. Due to copyright restrictions, Chapter 1 and Chapter 4 could not be included in this dissertation. For each of these chapters I provide a brief summary and associated DOI to the online article. Although I am listed as the sole author and use the pronoun I within this dissertation, each chapter was a collaborative effort and all associated manuscripts include one or more co-authors when submitted for peer-review.

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INTRODUCTION

The wildlife sciences are rapidly changing as the field continues to grow, advance, and embrace pressing challenges of the 21st century. Increased globalization, growing human populations and urban sprawl, and changing climate have precipitated swift environmental change and a concomitant suite of conservation issues (O'Brien and Leichenko 2000, McKinney 2002). As such, practitioners need to be adaptable and develop a diverse skillset capable of addressing these arising challenges. Currently, advances in technology and analytical tools have improved the ability of practitioners to meet conservation and management needs (Pimm et al. 2015). At the forefront of these challenges, there is need for effective management of non-native species, mitigation of conflict between human and wildlife populations, and broader understanding of species spatial ecology.

Invasion by non-native species is considered one of the greatest threats to global biodiversity, second only to fragmentation and habitat loss (Walker and Steffen 1997). Not only is invasion by non-natives detrimental to native flora and fauna, it also has substantial economic implications, where non-native species cost nearly $120 billion annually in the United States alone (Pimentel et al. 2005). Furthermore, introduction of non-native species is increasing from human trade and transport in an increasingly globalized market (Perrings et al. 2005, Meyerson and Mooney 2007). For these reasons, there is need for rapid response to non-native invasions as they are most effectively managed early during the invasion process (Simberloff 2003). Additionally, research into ecology of non-native species in recently colonized environments can provide important information to practitioners looking to effectively manage or eradicate non-native populations.

Another issue facing the wildlife sciences is human-wildlife conflict. Human-wildlife conflict can broadly be described as any action by humans or wildlife that is detrimental to the other (Conover 2002), caused by both native and non-native species. For example, wild pigs (*Sus scrofa*) are considered a nuisance species for their proclivity to root and overturn soil, resulting in damage to crops and residential property (Mayer 2009). Similarly, common forms of conflict for native species include crop-raiding by ungulates as well as livestock depredation by carnivores. These forms of conflict are especially evident in areas where humans and wildlife frequently interact, which occurs predominately in developing regions of the world. Furthermore, conflict also be intensifies in regions where pastoralism is a primary livelihood and livestock are culturally significant, making instances of depredation worthy of retaliation (Galaty 1982, Kissui 2008). Given severity of this conflict and potential for retaliation against wildlife, human-wildlife conflict presents a substantial threat to persistence and conservation of wildlife species (Woodroffe et al. 2005).

Recent advances in technological tools used in wildlife research and monitoring provides the ability to expand our understanding of how wildlife species function in space and time (Millspaugh and Marzluff 2001, Cagnacci et al. 2010, Tomkiewicz et al. 2010). Research on this topic can broadly be categorized as inquiries in spatial ecology, which aims to describe how spatial structure of the physical landscape influences species, populations, communities, and ecosystem function (Collinge 2010). Explorations in spatial ecology provide essential information that can be used to promote species conservation, as in European wildcats (*Felis silvestris*; Monterroso et al. 2009), two-toed (*Choloepus hoffmanni*) and three-toed sloths (*Bradypus variegatus*; Vaughan et al. 2007), and manta rays (*Manta birostris*; Stewart et al. 2016), among others. This information can also be used to manage and reduce spread of potentially harmful non-native species (With 2002, Glen et al. 2013). For these reasons, research aimed at better understanding spatial ecology of a species serves as an effective tool for conservation and management practitioners.

In this dissertation, I examine non-native species ecology and management, spatial ecology of native and non-native species, and human-wildlife conflict. To do this, I conducted research on three study systems and a broad range of taxa. In Chapter 1, I provide context for the non-native species component of my dissertation, where I review the behavior and spatial ecology of wild pigs in North America. In Chapter 2, I examine environmental impacts of an emerging, low-density population of wild pigs in Michigan. In Chapter 3, I explore wild pig movement ecology by identifying spatio-temporal correlates of wild pig movement states. In Chapter 4, I analyze the spatio-temporal dynamics of lion roaring in South Africa, in conjunction with a shift in dominance hierarchy. In Chapter 5, I analyze actionability of published human-carnivore conflict research as it relates to policy, management, and conservation action. I close this dissertation with concluding remarks and avenues for future research.

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CHAPTER 1:

BEHAVIORS AND SPATIAL ECOLOGY

We conducted a literature review of behaviors and spatial ecology of wild pigs in North America. In terms of behaviors, we described aspects of wild pig social organization, territoriality, rooting, diet, wallowing, rubbing and tusking, bedding, scent marking, and vigilance. For spatial ecology, we explored home range, habitat use and selection, activity and movement, and natal dispersal. Overall, wild pigs are a behaviorally plastic species that is highly adaptable to their surroundings. This adaptability is reflected in the spatial ecology of wild pigs, as this species can survive and thrive in a broad range of environments. In North America, research gaps remain as many behavioral and spatial studies occurred in native and/or international invasive ranges outside of the US. Specifically, additional research is needed on wild pig i) communication, ii) behavior and spatial ecology at fine spatio-temporal scales, iii) movement ecology, and iv) function in newly colonized areas, among others. This work is currently *in press* and will be included as a chapter in *Invasive Wild Pigs in North America: Ecology, Impacts, and Management*, published by CRC Press, Taylor and Francis Group, Boca Raton, Florida.

CHAPTER 2:

CAPACITY OF LOW DENSITY WILD PIGS AS EXOTIC ENGINEERS

2.1 Abstract

In North America, wild pigs (*Sus scrofa*) are a widespread non-native species capable of creating large-scale forest floor perturbations. Thus, wild pigs affect both biotic and abiotic properties of a system, characteristic of an exotic engineer. Given recent translocations of wild pigs to northern portions of the United States and Canada, research on impacts this species might have in northern systems is needed. Here, I assess impacts of wild pig disturbances on herbaceous plant communities, tree species, and soil chemistry in the central Lower Peninsula of Michigan. I selected 16 sites (8 ha) using GPS locations from seven wild pigs for sampling. I examined diversity of forest floor vegetation via Simpson's diversity index, impacts to tree regeneration, and collected soil cores from paired disturbed and undisturbed plots within each site. I observed less cover of native herbaceous plants and lower diversity, particularly for plants of high conservation value, in plots disturbed by pigs. I did not observe an increase in colonization of non-native plants following disturbance, though overall prevalence of non-native plants was low. Wild pigs did not exhibit selection for tree species when rooting, and I failed to find a significant effect of pig disturbances on regeneration of light- and heavy-seeded tree species. Magnesium and ammonium content in soils were lower in disturbed plots, suggesting soil disturbance accelerated leaching of macronutrients, potentially altering nitrogen transformation. This study demonstrates the capacity of wild pigs as exotic engineers at low densities and I discuss implications for northern systems of North America.

2.2 Introduction

Broadly, exotic engineers are non-native species that cause physical changes to biotic and abiotic components of an environment (Jones et al. 1994, 1997). Non-native species are considered a primary driver of global environmental change (Vitousek et al. 1997), posing serious threats to native ecosystems. There are several classic examples in which non-native species dramatically changed landscapes. For example, gypsy moth (*Lymantria dispar dispar*) invasions in North America resulted in large scale defoliation and changes to forest canopy structure (Fajvan and Wood 1996), release of understory vegetation (Bell and Whitmore 1997), and increased nest predation on forest-dwelling birds (Thurber et al. 1994). Invasion of parts of North America and Europe by nutria (*Myocastor coypus*) corresponded with decreased diversity of emergent plants (Nyman et al. 1993), lower nest success of indigenous waterbirds (Angelici et al. 2012), and concomitant loss of wetland area (Boorman and Fuller 1981, Kinler et al. 1998, Carter et al. 1999). However, impacts of exotic engineers are not always negative. In some instances non-native species indirectly benefit restoration efforts (Ferrero-Serrano et al. 2011) and provide ecological services that may have previously been lost (Ewel and Putz 2004). One species of particular interest as an exotic engineer is the wild pig (*Sus scrofa*), which, because of its rooting behavior, has potential to generate large scale perturbations capable of altering biotic and physical components of a system (Bratton 1975, Singer et al. 1984, Arrington et al. 1999, Tierney and Cushman 2006).

In the United States (US), wild pigs are considered a destructive invasive species, responsible for a conservatively estimated $800 million in damage annually (Pimentel et al. 2005). As omnivorous and dietary generalists (Senior et al. 2016), wild pigs thrive in a variety of habitats making them well-suited for invading new environments (Baskin and Danell 2003).

During foraging, wild pigs use their spade-like snouts to upturn soil in search of roots, tubers, invertebrates, and other subterranean food. Diets of wild pigs are predominately plant-based (Schley and Roper 2003, Ballari and Barrios-García 2014), though they also forage on a variety of vertebrates including amphibians and reptiles (Jolley et al. 2010), birds (Giménez-Anaya et al. 2008), small mammals (Wilcox and Van Vuren 2009), and carrion (Schley and Roper 2003). Consequentially, invasion by wild pigs pose risks to native flora and fauna, potentially resulting in cascading impacts to trophic interactions and ecosystem function. Overall magnitude and influence of these impacts will often vary by system and stage of invasion process, meriting further exploration in newly colonized areas.

Wild pigs occur in 38 US states and three Canadian provinces (Bevins et al. 2014, Brook and van Beest 2014). This distribution includes localized populations that recently appeared beyond the bounds of natural range expansion, likely due to commercial hunting interests (Courchamp et al. 2003, Long 2003) and unlawful introduction by people (Mayer 2009). This has resulted in emerging populations in northern portions of the US, which feature distinct vegetation communities, habitats, and climates. Though wild pigs exhibit characteristics of an exotic engineer in other portions of their range, consequences of their disturbances are less understood in newly colonized systems of the northern US where this species occurs at low densities. Additionally, northern systems in the non-native range of wild pigs may be more susceptible to wild pigs as exotic engineers because no functional analog for this species existed historically. Thus, these areas provide a unique opportunity to assess influences of wild pigs early during the invasion process, advancing understanding of the capacity of wild pigs as ecosystem engineers.

Wild pigs reduce plant cover (Singer et al. 1984, Rossell Jr et al. 2016), plant species richness (Bratton 1975, Rossell Jr et al. 2016), agricultural productivity (Bankovich et al. 2016), above-ground biomass (Ford and Grace 1998, Sweitzer and Van Vuren 2002), tree regeneration (Lipscomb 1989, Sweitzer and Van Vuren 2002), and ecosystem services (Pejchar and Mooney 2009). A potential outcome of wild pig disturbances is an invasion complex, where disturbances caused by a non-native species create opportunities for further establishment by other non-natives (Richardson et al. 2011). This phenomenon has been observed following wild pig disturbances, resulting in increased prevalence of non-native plants (Singer et al. 1984, Aplet et al. 1991, Siemann et al. 2009), but mechanisms contributing to this pattern require further exploration (Barrios-Garcia and Ballari 2012). Conversely, in some instances wild pigs positively influence plant species richness (Arrington et al. 1999) and growth (Lacki and Lancia 1986). Due to emerging numbers of wild pig populations in northern climates of North America, information on direction, magnitude, and extent of environmental impacts posed by this species is valuable. Furthermore, developing a better understanding of the capacity of wild pigs as an exotic engineer can aid in development of targeted mitigation strategies to address potential negative impacts to biotic and abiotic components most at risk in northern systems.

Here, I assessed impacts of wild pig disturbances on herbaceous plant communities, trees, and soil chemistry in the central Lower Peninsula of Michigan. I use the term disturbance throughout to refer to a combination of behaviors performed by wild pigs that may disrupt the forest floor (e.g., rooting, wallowing, digging). Via GPS-telemetry and public reports I selected areas of known pig occurrence to use in field sampling. I devised an experimental design to: *i*) compare ground-layer plant community composition and soil chemistry between disturbed and undisturbed plots, *ii*) assess influence of wild pig disturbances on non-native plant cover, diversity of native plant communities, and regeneration of light- and heavy-seeded tree species, and *iii*) examine wild pig disturbance around tree species. I use these results to assess the capacity of wild pigs as exotic engineers and their environmental impacts in northern portions of the US. I discuss implications of these results on short-term ecological impacts of disturbances from a low-density wild pig population in a northern, recently colonized environment.

2.3 Methods

2.3.1 *Study Area*

I conducted this study across 4 counties (Arenac, Bay, Gladwin, and Midland) in the central Lower Peninsula of Michigan (Fig. 2.1). Climate in this region is humid continental in that it experiences comparatively humid summers and cold winters. Average monthly temperatures range from -6.5 (January) to 20.8 ^{o} C (July) with average monthly precipitation highest in September (8.9 cm) and lowest in February (3.9 cm; Michigan State Climatologist's Office 2019). Forests in the southern portion of my study area consisted primarily of deciduous hardwoods (e.g., *Acer* spp., *Populu*s spp., *Quercus* spp.), while northern counties (i.e., Arenac and Gladwin) included conifer (e.g., *Pinus* spp., *Abies* spp., *Picea* spp.), mixed conifer, and hardwoods (Dickmann and Leefers 2016). Land cover in this region is primarily agriculture in the south with higher prevalence of forestlands in the north, with interspersed woody and emergent wetlands throughout. Soil moisture regimes tend to be aquic (i.e., saturated for periods long enough to reduce oxygen) and udic (i.e., moist soils of humid climates that receive consistent rainfall; USDA NRCS 2019), with soil temperatures ranging from mesic (i.e., 8 to 15 ^{o} C) to frigid (< 8 o C; USDA NRCS 2019). I conducted research on both state and privately owned lands with landowner permission.

Wild pigs were first reported in Michigan in 1999 (Johnson v. Creagh 2016) and occupied the state at low densities since (unpublished data USDA-APHIS). Though considered an invasive species throughout most of North America and in some locations naturalized (e.g., southeast US), here I refer to wild pigs as non-native given that populations in Michigan are characterized as emerging to transitional (Mayer 2009). The wild pig population in Michigan is unique in that most individuals display morphological characteristics comparable to those of Eurasian wild boar (*Sus scrofa* L.). In this way, Michigan wild pigs appear to differ from most other wild pig populations in the US, which tend to be comprised of feral domestics or hybrids (i.e., domestic x Eurasian wild boar).

2.3.2 *Site Selection*

From 2014 to 2016, I captured and equipped seven wild pigs (two-M, five-F) with IridiumTrackM collars (Lotek Wireless Inc., Newmarket, Ontario, Canada). All capture and handling protocols were approved by the Michigan State University Institutional Animal Care and Use Committee (01/14-013-00). I programmed collars to record GPS locations at 30-minute intervals, resulting in 22,172 GPS locations throughout this study area. Locations were accurate, with a mean dilution of precision of 2.74 (SE = 0.01). Bounded by the spatial extent of these locations, I overlaid a 285 x 285 m lattice (resolution = 8 ha) over the study area, and each cell of the lattice served as a potential sample area. I selected this resolution to approximate average patch size of forested vegetation and soil combinations in this study area (estimated to be ~11 ha). Within each cell I summed number of GPS locations (range 0 – 1,235) to serve as a proxy for intensity of use by wild pigs, where I hypothesized that cells with higher intensity of use would correspondingly contain greater amounts of disturbance by wild pigs. When selecting sites, I stratified sampling across various potential levels of disturbance intensity informed by the number of GPS locations within a cell.

2.4 Biotic Components

2.4.1 *Vegetation Assessments*

Within each 8 ha site I surveyed a network of nine transects (each 240 m long) oriented north-south and spaced 30 m apart. I selected a 240 m transect distance because it represents the maximum length within each 8 ha site. Every 30 m along each transect I established a 2 m radius plot, resulting in 81 sampling plots per site. I divided plots into four quarters, with each quarter serving as a sub-sample at the plot-level. In each quarter plot I noted presence (1=disturbed, 0=undisturbed), intensity (depth in cm), and percentage of wild pig disturbance. Field crews had extensive experience differentiating wild pig disturbance (particularly rooting) from other potential sources of disturbance to the forest floor. In most instances, disturbance by wild pigs exceeded that of native fauna (e.g., raccoon─*Procyon lotor,* striped skunk─*Mephitis mephitis,* wild turkey─*Meleagris gallopavo*) in both depth and surface area.

At every fourth plot within a site (20 total) I randomly placed 2 - 1 m^2 Daubenmire frames (Daubenmire 1959) to measure vegetation coverage (%) of woody and herbaceous plants by species. I placed frames ≥ 1 m from plot center to ensure spatial separation between paired frames. Trees or shrubs ≥ 2 m in height were not considered part of the forest floor and I excluded them from Daubenmire assessments. For plants not identifiable in the field, I recorded finest level of taxonomy and photographed the specimen for later identification. Due to difficulty in differentiating among species of grasses and sedges, I broadly grouped these by family and did not seek finer taxonomic classification. In my second field season (2017), I revisited sites and conducted vegetation assessments at paired disturbed and undisturbed plots not previously sampled to broaden characterization of the site and temporal resolution of collected data.

2.4.2 *Tree and Shrub Assessments*

As wild pigs frequently root near the base of trees (Sanguinetti and Kitzberger 2010), I examined relationships between wild pig disturbance and potential impacts to various tree and shrub species. Here I considered any disturbance occurring near the stem of a tree or shrub (≥ 2 m in height) as potentially damaging, as this could directly impact the root system. I used a point-centered quarter method (Cottam and Curtis 1956) at each plot (81 per site) to characterize the tree and shrub community, and recorded evidence of disturbance within 2 m of the stem, species, and distance to plot center.

2.5 Abiotic Components

2.5.1 *Soil Assessments*

I examined soil chemistry of paired disturbed and undisturbed plots within each site in 2017. For sites that were disturbed at > 3 plots, I collected soil at three paired plots and every 3rd plot thereafter. Sampling within sites was stratified to account for soil types using the Soil Survey Geographic (SSURGO) database for soil classification (Soil Survey Staff 2016). At each location, I extracted three soil cores at a depth of 30.5 cm (diameter = 1.9 cm) and placed each sample into a plastic Ziploc® bag for transport. In disturbed plots, I extracted samples directly from areas with overturned soil. I mixed samples obtained from the same site, disturbance (i.e., disturbed and undisturbed) and soil type combination in a plastic bucket to create a composite sample for testing. I created composite samples because more consistent laboratory results are obtained as samples increase (Shickluna and Robertson 1987). I cleaned tools used for mixing samples between each use. I tested for pH and content of macronutrients (potassium, calcium, magnesium). In addition, I examined phosphorus (P) using the Bray-1 extraction method (Bray and Kurtz 1945). For mineral nitrogen, I assessed ammonium and nitrate content of each sample. I selected these soil properties as they are readily quantified and the most likely to be influenced by wild pig disturbances. For example, disturbances by wild pigs alters nitrate concentrations and accelerates leaching of macronutrients (Singer et al. 1984, Mohr et al. 2005).

After collection, I promptly stored soil samples in a cooler and later transferred them to a freezer. I dried soil samples in an oven at 38^{o} C until all moisture was removed and then finely ground and sieved (2 mm) each sample. I used soil-testing protocols designed and approved by the Michigan State University Soil and Plant Nutrient Laboratory.

2.6 Data Analysis

I explored relationships between prevalence and extent of wild pig disturbances and land cover classes using 2011 National Land Cover Database (NLCD; Homer et al. 2015). I also extracted elevation, slope, drainage, and soil type from the SSURGO database for each plot. To examine impacts of wild pig disturbance on forest floor plant communities I ordinated plot-level percent cover of plant species using non-metric multi-dimensional scaling (NMDS), as this method allows for ordination of heterogeneous community data (McCune and Grace 2002). Ordinations were implemented using the *vegan* package (Oksanen et al. 2013) developed for descriptive community ecology in *R* (version 3.5.0). I initially conducted an ordination using all vegetation before parsing data by physiognomy, resulting in independent ordinations of woody and herbaceous vegetation. For each ordination, I maintained stress under a threshold of 0.15, as this level is considered reasonable for interpreting patterns in community data (Clarke 1993). To further explore separation of vegetation communities in ordination space, I applied a general additive model (GAM) using proportion of disturbance within a plot as an explanatory variable. I report the deviance explained and display resulting GAM contours within two dimensional ordination plots.

I also explored impacts of wild pig disturbances on forest floor plant diversity in disturbed and undisturbed plots. I analyzed diversity of native plant cover, plants with a coefficient of conservatism ≥ 5 (Herman et al. 1997), and light and heavy seeded tree species. Species with a coefficient of conservatism ≥ 5 are considered obligates to natural areas, though these areas may not reflect pre-settlement conditions (i.e., are degraded; Herman et al. 1997). Light and heavy seeded tree species have different reproductive and germination strategies affected by disturbances to the forest floor. Additionally, heavy seeded tree species like oak (*Quercus* spp.) and beech (*Fagus grandifolia*) provide nuts that are highly sought food items by wild pigs. I calculated Simpson's diversity index (Simpson 1949):

$$\lambda = 1 - \sum s \frac{n_i(n_i - 1)}{N\,(N-1)}$$

Here, n_i refers to percent cover of individuals belonging to the *i*th species and *N* is the total percent cover of individuals of all species (*s*). Simpson's index was appropriate for this study as it is robust to small sample sizes (Lande et al. 2000). I calculated Simpson's diversity indices between disturbed and undisturbed plots within a site.

I implemented a use versus available resource selection framework (Manly et al. 2002), calculating a Manly selectivity index and chi-square analysis using the "adehabitatHS" package in *R* (Calenge 2015) to evaluate if pigs selectively rooted at the base of certain tree species. I plotted selection indices and confidence intervals for each tree species. In this case, confidence intervals above and not overlapping one are indicative of selection, whereas values falling below this threshold indicated avoidance. Tree species with confidence intervals that overlapped one were selected proportionally to their availability (Desbiez and Bodmer 2009). I used each plot within a site as a replicate, for 1,296 total records.

For comparisons of plant diversity and soil characteristics between disturbed and undisturbed plots, I conducted a Welch's two-sample *t*-test to explore whether these metrics significantly differed due to wild pig disturbance. I calculated Simpson's index at the site level and displayed site-level diversity indexes by disturbance type using box and whisker plots. I also report the corresponding p-values and confidence intervals for each test.

2.7 Results

During the summers of 2016 and 2017, I conducted environmental assessments at 16 sites where wild pig disturbances were observed. I found that the number of wild pig GPS locations within a site was not a reliable predictor of disturbance extent (Fig. 2.2). On average, 12% (SE = 1.44) of plots within a site were disturbed with a minimum of 2% and maximum of 21% (Fig. 2.2). The amount of area disturbed within each plot was variable, ranging from localized patches < $1m^2$ to more expansive disturbance that covered the entirety of the plot. Disturbance was relatively shallow, averaging 3.6 cm (SE = 0.3), but I recorded depths of 28 cm. Disturbed plots occurred at an average elevation of 265 m (SE = 7.96) and slope of 3% (SE = 0.22). Disturbance occurred most often in deciduous forests (63%) and woody wetlands (26%), with trace occurrences in developed, mixed forest, shrub/scrub, grassland, and emergent herbaceous wetland cover types. Plots were disturbed an estimated average of 584 days prior to sampling, with a minimum of 259 and maximum of 853 days.

2.8 Biotic Components

2.8.1 *Vegetation Assessments*

I conducted vegetation assessments at 320 plots in 2016 and 132 in 2017. In total, I observed 155 plant species during vegetation assessments. Common herbaceous plant species encountered in plots included: grasses (Poaceae), sedges (Cyperaceae), wild lily-of-the-valley (*Maianthemum canadense*), bracken fern (*Pteridium aquilinum*), star-flower (*Trientalis borealis*), and sensitive fern (*Onoclea sensibilis*). I observed a lower percent herbaceous plant cover in disturbed (23.66%, SE = 0.95) compared to undisturbed plots (52.27%, SE = 0.54).

Ordinations of percent cover of all plant species in disturbed and undisturbed plots displayed minimal separation between disturbed and undisturbed plots in ordination space (stress = 0.13; Fig. 2.3). Percent of the Daubenmire frame disturbed as the explanatory variable in GAM was responsible for 8.4% of the deviance explained. Hence, disturbance by wild pigs did not substantially influence overall plant community composition of the forest floor. Ordination of percent cover of woody plant species also revealed minimal separation between disturbed and undisturbed plots (stress = 0.14; Fig. 2.4), with percent area disturbed GAM explaining 2.8% deviance. Disturbance by wild pigs did not appear to impact the woody plant community of the forest floor. Conversely, herbaceous plant species showed distinct separation and clustering between disturbed and undisturbed plots (stress = 0.05; Fig. 2.5), and GAM modelling of percent area disturbed accounted for 73.6% of deviance explained.

Site-level Simpson's diversity index of native herbaceous vegetation cover was similar among undisturbed and disturbed plots ($P = 0.12$; Fig. 2.6). However, diversity of herbaceous plant species cover with a coefficient of conservation ≥ 5 was significantly greater in undisturbed than disturbed plots ($P = <0.01$; Fig. 2.6). I failed to find enough non-native plant species to conduct a reliable comparison between disturbed and undisturbed plots (Fig. 2.6). Diversity of seedlings from light and heavy seeded tree species was generally higher for both reproductive strategies in undisturbed plots, however, this difference was not statistically significant (P = 0.09, P = 0.70, respectively; Fig. 2.6).

2.8.2 *Tree and Shrub Assessments*

I identified 336 individual trees or shrubs and 24 species that had disturbance <2m from the stem. Wild pig disturbance was recorded most often near red maple (*Acer rubrum*), white pine (*Pinus strobus*), and witch-hazel (*Hamamelis virginiana*), but specific species were not selected for (Fig. 2.7). Conversely, wild pigs avoided rooting near northern pin oak (*Q. ellipsoidalis*) and speckled alder (*Alnus incana*; Fig. 2.7).

2.9 Abiotic Components

2.9.1 *Soil Assessments*

I observed disturbance most often in soils considered sandy, and moderately- to poorly-drained. The taxonomic orders of soils that were most often disturbed were Spodosols (rich in aluminum oxide and organic matter) followed by Entisols (undifferentiated mineral soils), with fewer occurrences in both Histosols (peaty soils, deep organic layer) and Mollisols (dark, humus rich surface layer with high calcium and magnesium). I collected 68 composite soil samples across 16 sites and 14 soil types. Welch's *t*-tests for group differences among soil characteristics in disturbed and undisturbed plots within a site did not yield significant differences in pH, phosphorus, potassium, or nitrate. Though not statistically significant at $P \leq 0.05$ threshold, results for calcium were marginal (P = 0.07), with soils in undisturbed plots containing greater amounts of calcium. Similarly, soils in undisturbed plots contained significantly higher quantities of magnesium (P = 0.03) and ammonium (P = 0.01) than disturbed plots (Table 2.1).

2.10 Discussion

I explored impacts of wild pig disturbances on environmental variables in the central Lower Peninsula of Michigan. I caution that these findings derive from relatively recent (within ~2 years) plant and soil responses to wild pig disturbances. Thus, I recommend longer-term monitoring to develop a holistic understanding of environmental impacts posed by wild pigs in the northern US. However, the temporal window in this study is sufficient for measuring impacts to plant colonization, persistence, and regeneration while subsequently limiting other potentially confounding sources of disturbance. I found that wild pig disturbances effectively altered structure and composition of herbaceous plant communities within ~2 years of the disturbance event. Wild pigs are unique in this landscape given their ability to create forest floor disturbances that exceed that of native fauna in both depth and extent in Michigan. The only comparable disturbances in this area could be attributed to humans (e.g., logging, agriculture). Although I did not record evidence that wild pig disturbances facilitated colonization of non-native species, I observed less cover of native herbaceous plants and lower diversity in disturbed plots, a trend particularly evident for plants of higher conservation value. Typical of a generalist, I did not detect evidence that wild pigs exhibited selection for specific tree species when rooting. I suspect that wild pigs were instead motivated by alternative sources of subterranean forage (e.g., invertebrates, fungi, seed middens). While not statistically significant, regeneration of light and heavy seeded tree species tended to be lower in disturbed plots. Magnesium and ammonium were significantly lower in disturbed plots, suggesting that soil rooting accelerates leaching of macronutrients and potentially alters nitrogen transformation processes. Results indicated that wild pigs, even at low densities, have the capability to alter biotic and abiotic features in a landscape, consistent with criteria of an exotic engineer. I found that even low-density wild pig populations pose detrimental consequences to northern ecosystems of the US.

Disturbances by wild pigs had the strongest impact on herbaceous plants by reducing overall cover, consistent with other studies (Bratton 1975, Singer et al. 1984, Arrington et al. 1999, Cole et al. 2012, Cuevas et al. 2012). Disturbances by wild pigs also altered composition and structure of herbaceous plant communities, apparently a function of amount of disturbance within a plot. This aligns with previous research exploring impacts of disturbances on plant communities in high-density wild pig areas including California (Cushman et al. 2004), Hawaii (Aplet et al. 1991), and the Great Smoky Mountains (GSM; Bratton 1974). Furthermore, diversity assessments indicated that wild pig disturbances posed significant negative consequences to herbaceous plant species of high conservation value. These plants often depend on natural disturbances (e.g., tree fall gaps) or relatively undisturbed environmental conditions, and wild pig disturbances appeared to limit colonization and survival over the short term. Similar to my findings, negative impacts to rarer plant communities by wild pigs have been documented in Florida (United States Department of Agriculture 2002) and California (Santa Cruz Island; National Park Service 2002).

I did not observe differences in structure and composition of woody plant species between disturbed and undisturbed plots. This result may be due to the relatively short-duration of this study, which occurred over a span of ~2 years (from disturbance to field measurements). I expected to see increases in germination of light-seeded tree species in disturbed plots, as rooting exposed mineral soil. I also anticipated pronounced, adverse responses in regeneration of heavy seeded tree species to wild pig disturbance. In California, disturbance by wild pigs was shown to hinder oak regeneration through seed predation, and reductions in seedling size and survival

(Sweitzer and Van Vuren 2002, 2008). Similar effects to regeneration of heavy seeded tree species were reported in the native range of wild pigs (Bruinderink and Hazebroek 1996, Gómez et al. 2003). Within two years of disturbance, I found similar levels of tree regeneration for both light and heavy seeded species in disturbed and undisturbed plots. Impacts to tree regeneration appear to be more pronounced in areas with high-density pig populations (Sweitzer and Van Vuren 2002), potentially revealing why I did not observe stronger responses in this study.

Similar to other studies, I observed disturbance at or near the base of trees and shrubs, which often exposed parts of the root system (Singer et al. 1984). This process can expose root systems to drying and insect or disease infections, potentially compromising tree vigor. Wild pigs did not select for tree or shrub species when rooting in Michigan. This result suggests that rooting behavior is not directly related to fruit or mast produced in the crown or canopy, but rather, some other form of subterranean forage consistent with findings in beech forests of the GSM (Bratton 1975). Potential alternative below ground food sources influencing rooting behavior include fungi (Baubet et al. 2004, Skewes et al. 2007), invertebrates (Baubet et al. 2003), and small mammal caches (Focardi et al. 2000, Gómez et al. 2003). I hypothesize that much of the intensive rooting observed directly at the base of trees was done to exploit small mammal caches (Suselbeek et al. 2014), as deep excavations are often performed by wild pigs with the purpose of pilfering caches when other forage is scarce (Focardi et al. 2000).

I also found considerable variation in the impacts of wild pig disturbance on soil chemistry. Most notably, I observed a reduction in magnesium and ammonium in disturbed soils. Magnesium is essential for plant (Wilkinson et al. 1990), animal (Kruse and Orent 1932), and microbial communities (Fulmer 1918). In plants, magnesium is primarily obtained from soils and is necessary for plant growth (Cakmak et al. 1994a, Cakmak and Yazici 2010) and protein synthesis (Cammarano et al. 1972, Sperrazza and Spremulli 1983). Magnesium also plays a role in plant immune systems and reduces tissue degradation by soft rotting pathogens (Huber and Jones 2013). Reduction of magnesium in soils following disturbance is expected, as magnesium is readily leached through soil weathering (Mayland and Wilkinson 1989). Reductions in magnesium following wild pig disturbances were also observed in GSM (Singer et al. 1984).

Several studies explored rooting impacts to soil ammonium, generally finding that levels of ammonium were similar in both disturbed and undisturbed soils (Cushman et al. 2004, Siemann et al. 2009, Cuevas et al. 2012). I found significantly less ammonium in disturbed soils in contrast to results found in the GSM (Singer et al. 1984). Accumulation of ammonium in soils may arise under multiple conditions when nitrogen conversion is limited. Examples of these conditions include when soils have a lower pH, reduced oxygen, lack organic material, limited soil moisture, and/or low temperatures (Mengel et al. 2001). My findings suggest that disturbances by wild pigs may alter and potentially accelerate nitrogen transformation processes, although I would expect a concurrent increase in nitrates, which I did not observe. I proffer that lower ammonium content in disturbed soils is a remnant of the physical disturbance to the ground layer, which aerates soils and alters soil temperature and moisture content.

Though widely considered an ecosystem engineer, overall direction and magnitude of environmental changes caused by wild pigs in northern systems of the US was largely unknown. Some have advocated for exploring potential roles and benefits of non-native species (Schlaepfer et al. 2011), with some successes relevant to wild pigs (see Gawel et al. 2018). Results indicated that wild pigs indeed fit the role of an exotic engineer, with most induced changes impacting herbaceous plant communities and chemical properties in soils. In this study, wild pig disturbance did not facilitate colonization of non-native plant species, as suggested by invasion complex theory. Incidence of non-native plant species in this study was relatively low, with this result potentially more pronounced in landscapes heavily dominated by non-native plants. While the magnitude of some environmental effects I observed in this study were subtle, results suggest that even at low densities and early in the invasion process, wild pigs have the ability to alter biotic and abiotic components in northern systems.

2.11 Acknowledgements

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APPENDIX

Table 2.1.

Mean (SE) soil attributes collected at disturbed and undisturbed plots in 8 hectare sites (n=16) disturbed by wild pigs (*Sus scrofa*) in the central Lower Peninsula of Michigan, 2016-2017.

Soil attributes	Disturbed	Undisturbed	*P*
pH	5.61 (0.11)	5.41 (0.13)	0.25
Phosphorus (%)	13.50 (1.36)	13.44 (1.18)	0.97
Potassium (ppm)	47.59 (2.19)	52.32 (2.51)	0.16
Calcium (ppm)	865.09 (149.69)	1289.12 (176.14)	0.07
Magnesium (ppm)	107.72 (13.93)	164.03 (20.35)	0.03*
Nitrate (NO_3; ppm)	7.53 (0.91)	8.00 (0.86)	0.71
Ammonium (NH_4; ppm)	10.78 (0.99)	16.39 (1.91)	0.01*

* denotes significance at the 0.05 threshold based on Welch's *t*-tests for group differences

Figure 2.1.

Four county (Arenac, Bay, Gladwin, Midland) study area in the central Lower Peninsula of Michigan, USA, where environmental impacts of wild pig disturbances were studied.

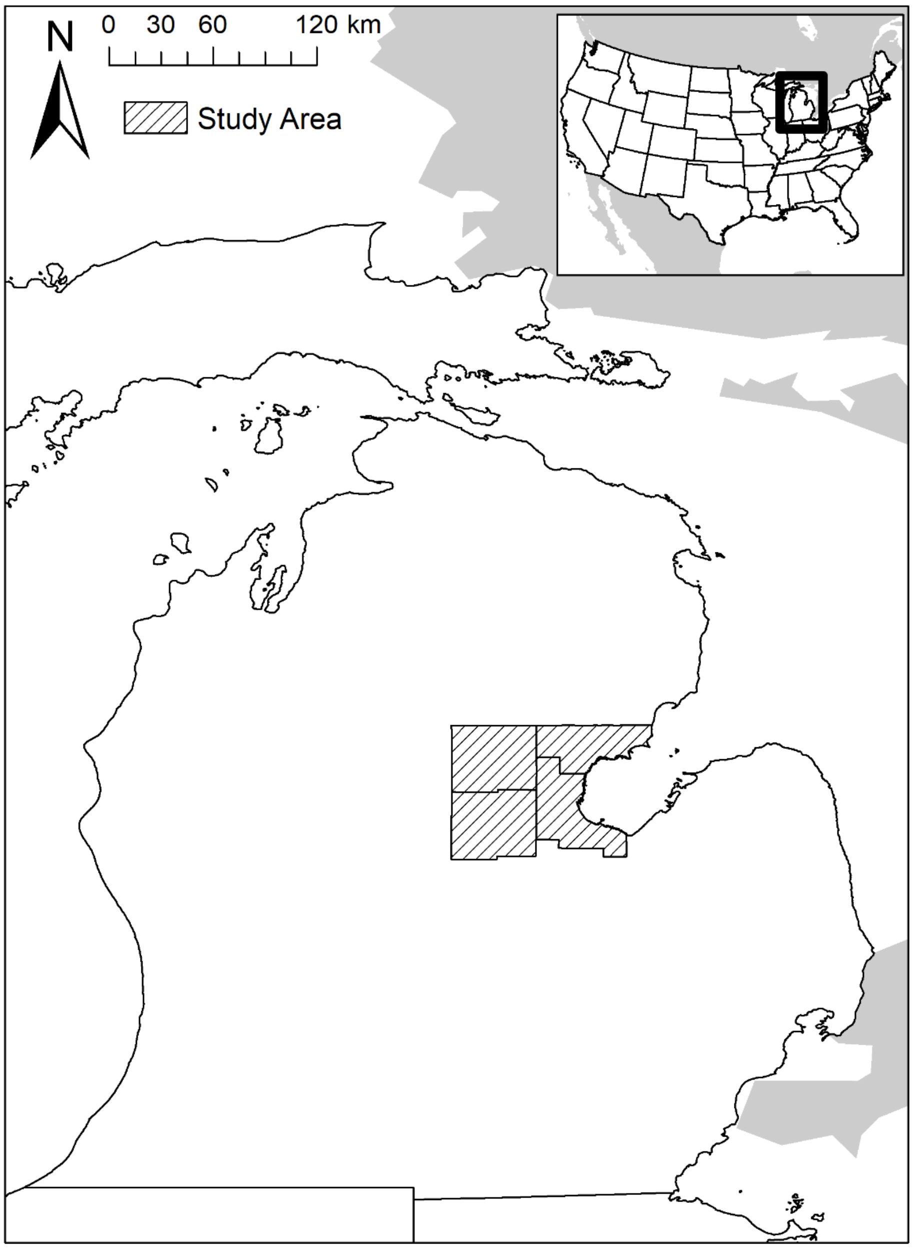


Figure 2.2.

Relationship between percent disturbed plots in 8 ha site (n=16) and number of corresponding wild pig (*Sus scrofa*) GPS locations, 2016-17, in the central Lower Peninsula of Michigan, USA.

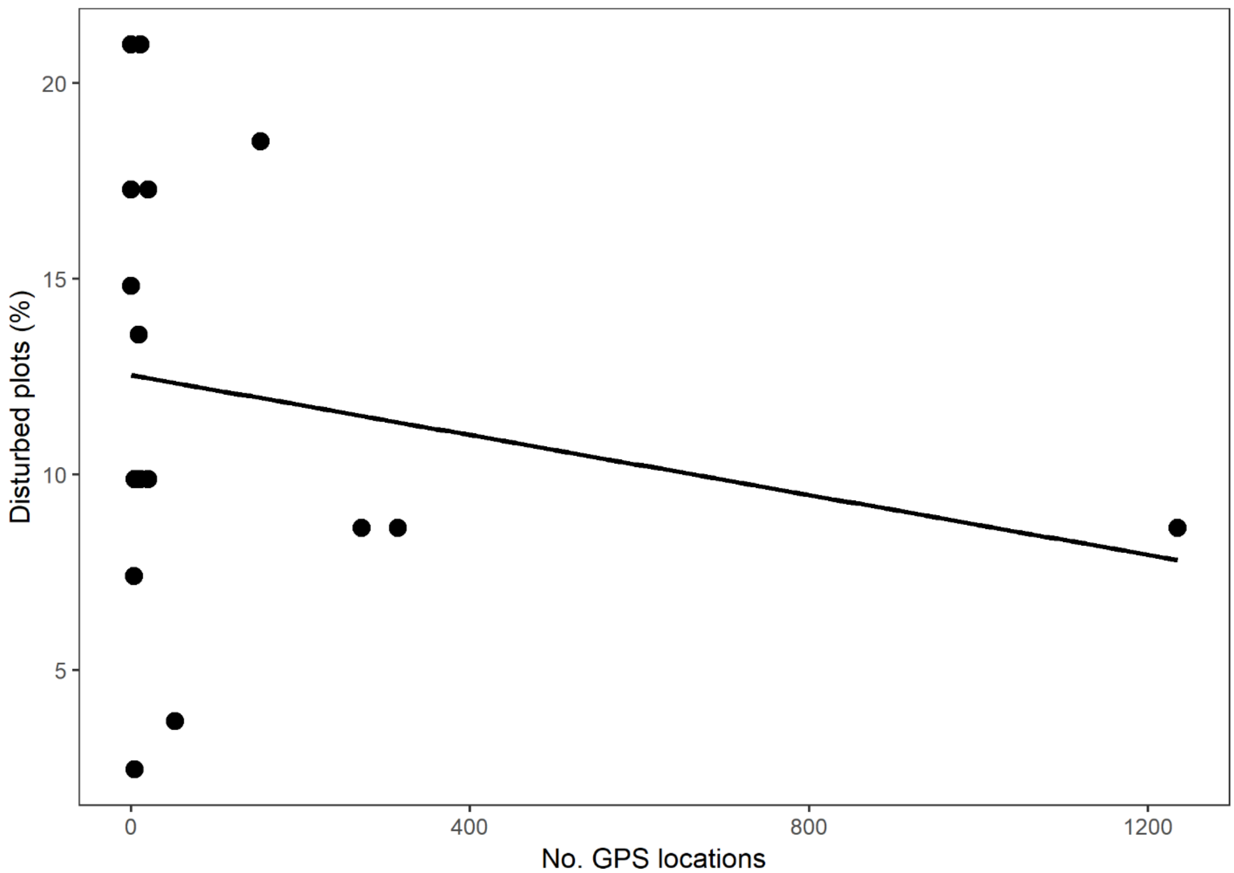


Figure 2.3.

Non-metric multidimensional scaling of percent cover of forest floor plants in plots disturbed by wild pigs (*Sus scrofa*) and undisturbed plots from 16 sites (2016-17) in the central Lower Peninsula of Michigan, USA. Contours depict the percent area disturbed within plots, used as the response variable in general additive modeling.

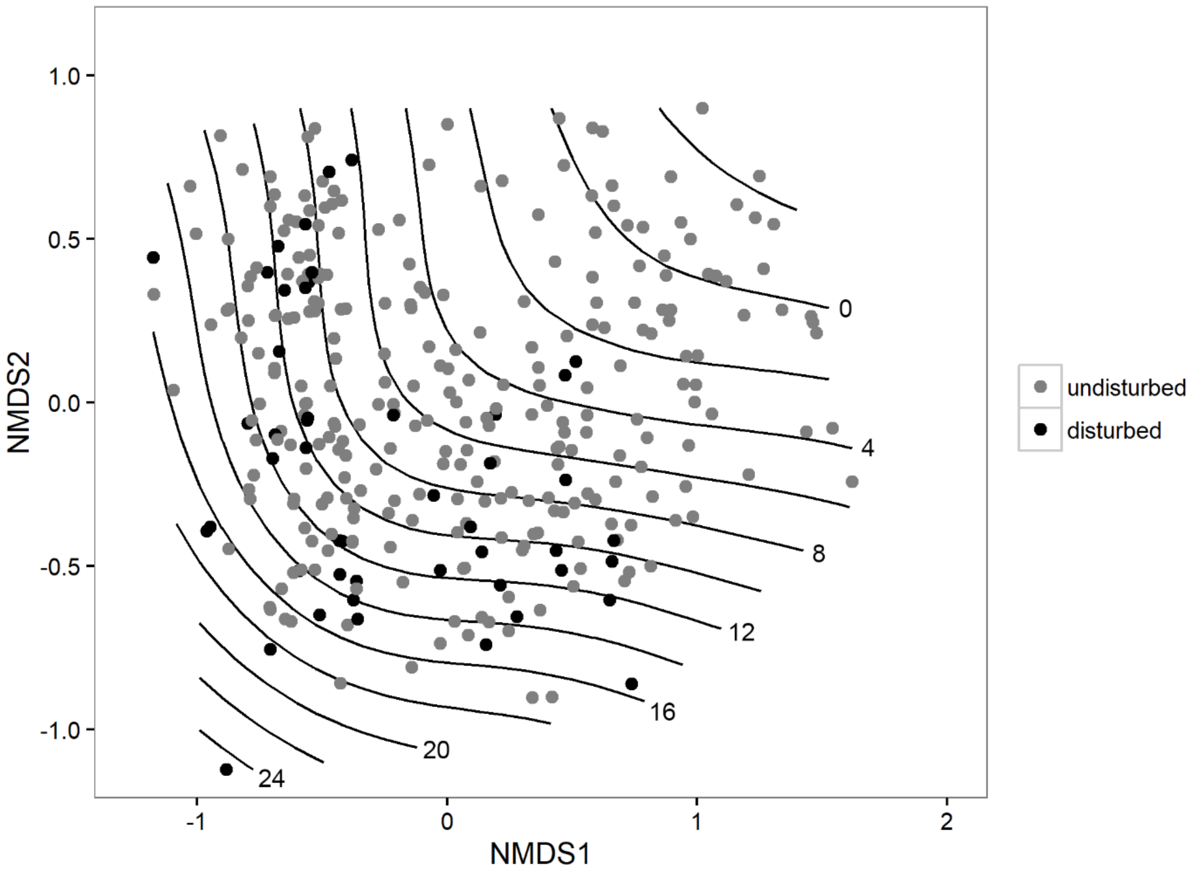


Figure 2.4.

Non-metric multidimensional scaling of species percent cover of woody vegetation communities in plots disturbed by wild pigs (*Sus scrofa*) and undisturbed plots in 16 sites during 2016-17 in the central Lower Peninsula of Michigan, USA. Contours depict the percent area disturbed within plots, used as the response variable in general additive modeling.

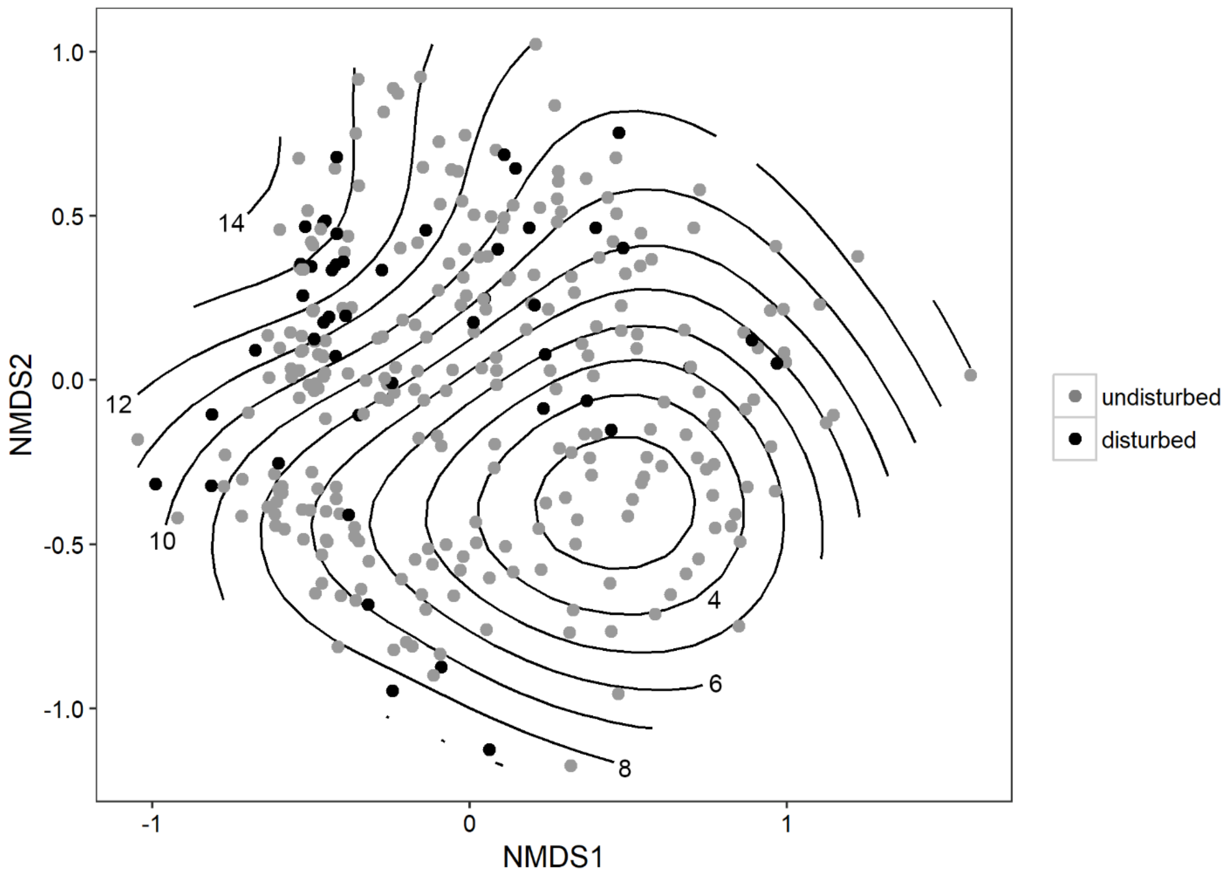


Figure 2.5.

Non-metric multidimensional scaling of species percent cover of herbaceous vegetation communities in plots disturbed by wild pigs (*Sus scrofa*) and undisturbed plots in 16 sites during 2016-17 in the central Lower Peninsula of Michigan, USA. Contours depict percent area disturbed within plots, used as the response variable in general additive modeling.

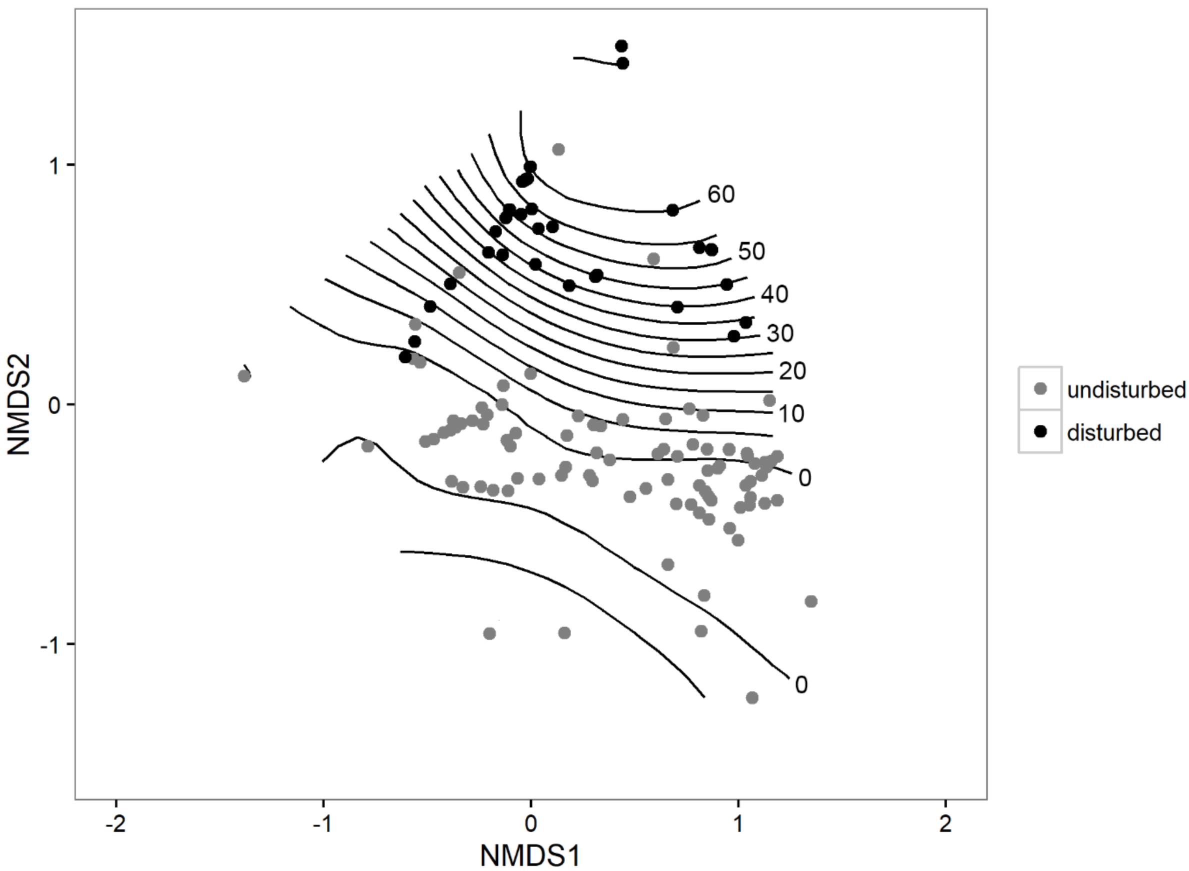


Figure 2.6.

Site-level (n=16) Simpson's diversity index in plots disturbed by wild pigs (*Sus scrofa*) and undisturbed plots in the central Lower Peninsula of Michigan, USA, 2016-17. Horizontal lines within boxes represent medians, boxes represent interquartile ranges, and whiskers represent 95% confidence intervals. Significant *P*-values from Welch's two sample *t*-tests denoted by an asterisk. Native = native herbaceous plant species; CC = herbaceous species with a coefficient of conservation ≥ 5; Non-Native = non-native herbaceous plant species; Light = light seeded tree species; Heavy = heavy seeded tree species.

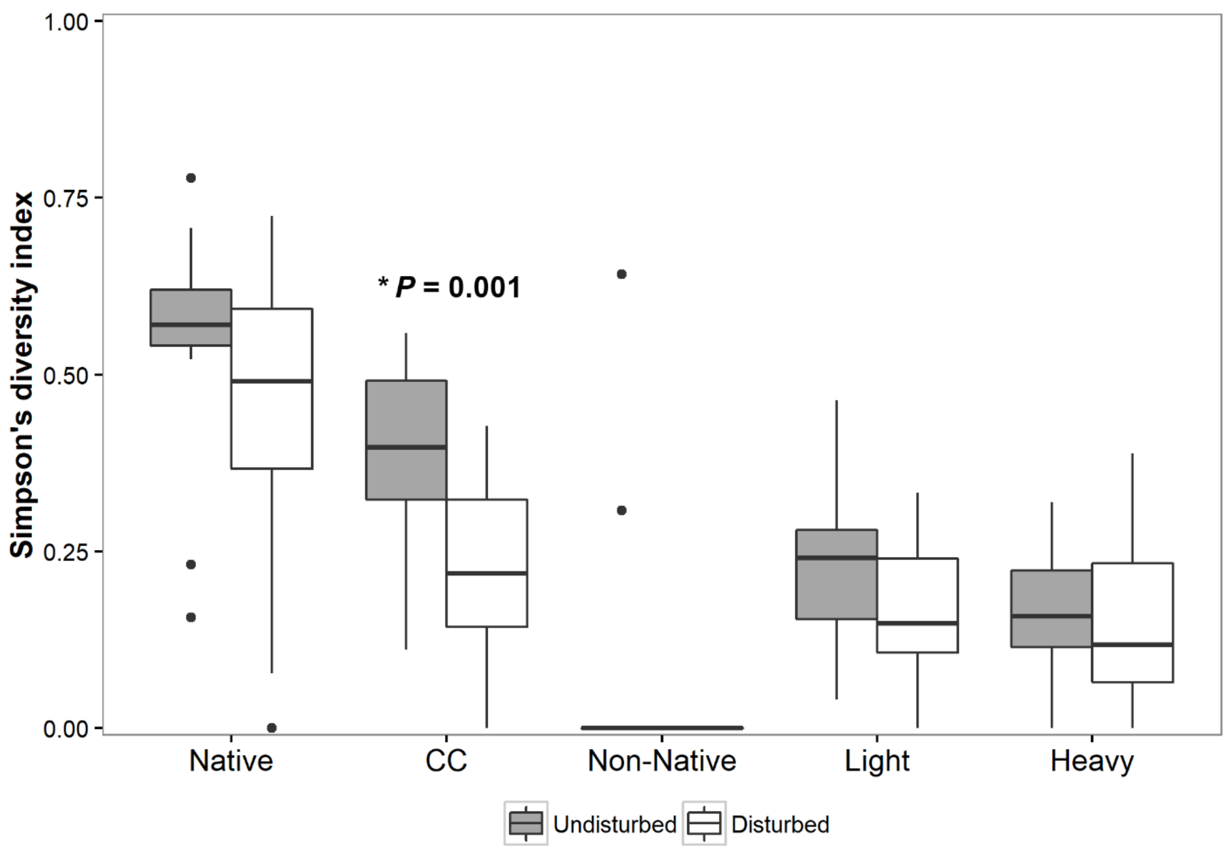
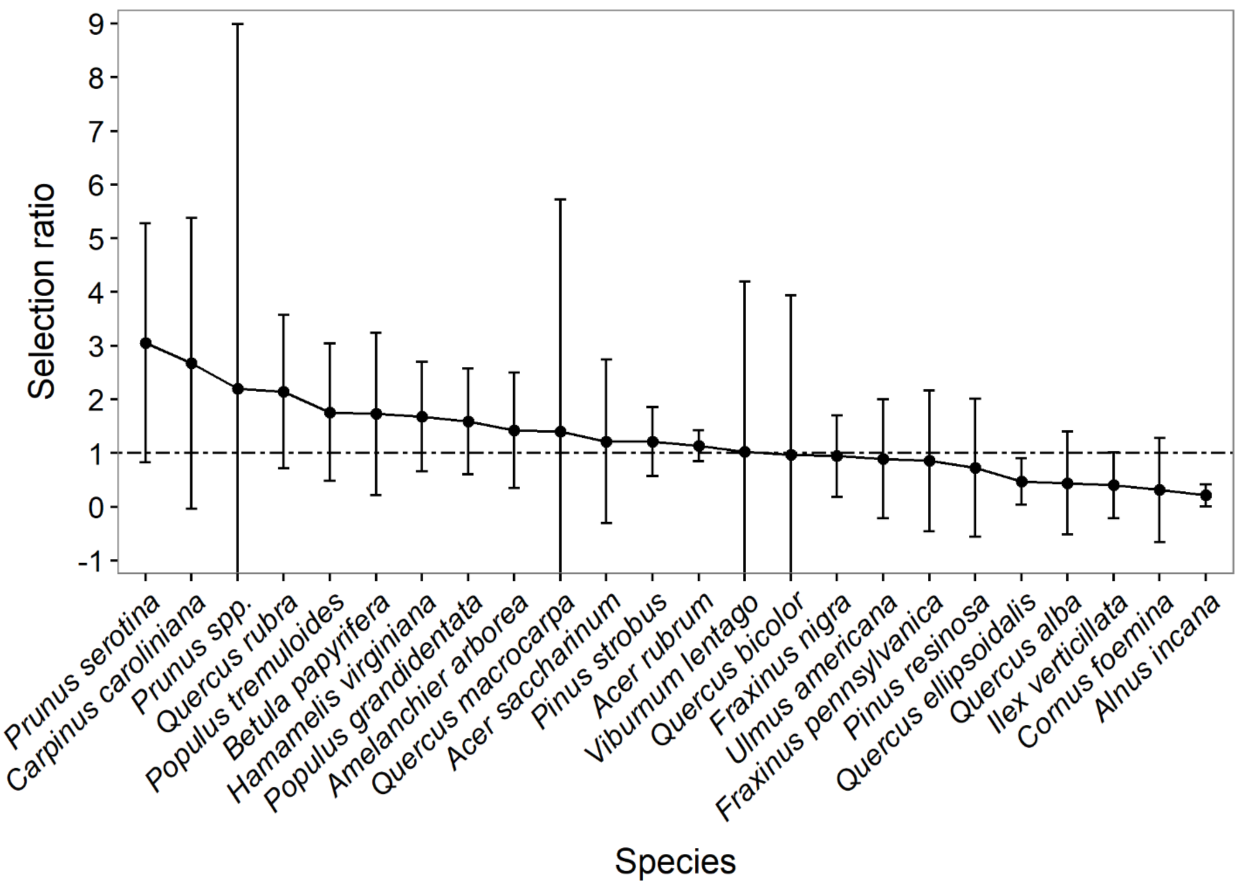


Figure 2.7.

Manly selectivity index of wild pig (*Sus scrofa*) disturbances and tree species in 2016 in the central Lower Peninsula of Michigan, USA. Values above the dashed horizontal line indicate selection for and values below indicate avoidance. Bars represent 95% confidence intervals.



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CHAPTER 3:

SPATIO-TEMPORAL CORRELATES OF STATES OF WILD PIG MOVEMENT

3.1 Abstract

Movement is an essential element of animal ecology as it governs a wide array of ecological and evolutionary processes. Research on movements and behaviors related to biotic and abiotic components of a system, improves understanding of the distribution and ecology of non-native and invasive species. Predictions of models describing these animal-habitat associations can be used to prioritize implementation of management activities. Here I explored the movement ecology of a low-density, invasive wild pig (*Sus scrofa*) population in the state of Michigan, US. Using data returned from GPS-tracking of ten wild pigs over a four-year period I quantified wild pig movement states (e.g., moderate movement – high fidelity (MM-HF), low movement – moderate fidelity (LM-MF), and rapid movement – low fidelity (RM-LF)), assessed biotic and abiotic conditions that correlated with these states, and predicted probability of these movement states across the landscape. I found that spatial configuration of these movement states was a function of land cover type proportions, landscape structure, and weather conditions. Probability of MM-HF was positively related to cohesion of shrub cover types, which may be important visual and thermoregulatory refuge in winter. The LM-MF state mostly coincided with increasing patch cohesion of agricultural cover types, suggesting importance of this cover type in forgaing. Probability of RM-LF was primarily driven by proportion of human development, with an increasing likelihood of larger movements in human-dominated areas. This analysis outlines a rigorous comparison of wild pig movement states in relation to biotic and abiotic conditions. I

discuss implications of this research for the ecology, function, and management of wild pigs in northern systems of the US.

3.2 Introduction

Movement is a fundamental component of animal ecology. Animals move in pursuit of forage (Mårell et al. 2002, Brooks and Harris 2008, Fryxell et al. 2008), to decrease probability of encountering predators (Rettie and Messier 2001, Mitchell and Lima 2002, Frair et al. 2005, Moriarty et al. 2016, Weterings et al. 2016), to select resting sites (Maillard and Fournier 1995, Brown et al. 2014, Larroque et al. 2015, Wittemyer et al. 2017), and to avoid sources of disturbance (Pruett et al. 2009, Leblond et al. 2013, Stillfried et al. 2015), among other reasons. Given the fitness implications associated with these behaviors, movement is critical to the structure and function of populations, animal communities, and trophic systems, more broadly (Swingland and Greenwood 1983, Dingle 1996, Hanski 1999, Bullock et al. 2002, Greenberg and Marra 2005). Thus, research into animal movement serves as a cornerstone of many ecological inquiries.

Recent growth in research on various aspects of animal movement has followed growth of advanced animal tracking technology capable of yielding increasingly resolute locational data (Millspaugh and Marzluff 2001, Cagnacci et al. 2010, Tomkiewicz et al. 2010). Furthermore, simultaneous advances in conceptual frameworks and analytical tools in which to better understand movement processes occurred (Morales et al. 2004, Nathan et al. 2008, Long and Nelson 2013). Emergent research demonstrated that movement states of animals can be inferred from GPS telemetry locations and subsequently linked to specific behaviors (e.g., resting, foraging; Morales et al. 2004, Patterson et al. 2008, Van Moorter et al. 2010). Furthermore, as transitions between movement states are governed by behavioral responses to biotic and abiotic conditions in a given area (Zhivotovsky et al. 1996, Forester et al. 2007, Nathan et al. 2008, Revilla and Wiegand 2008), exploration of external factors influencing these transitions are of ecological interest. Predicting movement states via quantification and understanding of spatio-temporal structure of these conditions can provide valuable information to inform prevailing conservation and management practices.

Linking movement and behavioral states to biotic and abiotic conditions may be particularly relevant to species that are non-native and invasive, thereby facilitating control or eradication. Take, for example, emerging populations of wild pigs (*Sus scrofa*) in northern landscapes of North America. These populations are relatively new to this region (e.g., established in the last 20 years), and many are products of inadvertent or unlawful introductions by people and escapees from private hunting reserves (Mayer 2009, Johnson v. Creagh 2016). Unlike many wild pig populations in the southeastern United States (US) that are principally comprised of feral domestics and hybrids (i.e., typically the offspring of domestic pigs and Eurasian wild boars), wild pig populations in northern systems are primarily composed of individuals that are morphologically and genetically similar to Eurasian wild boars (Smyser et al. personal communication), perhaps representing movement and behavioral differences. Wild pigs are destructive and economically-harmful and pose important disease risks to livestock (Pimentel et al. 2005, Gortázar et al. 2007, Ruiz-Fons et al. 2008), damage to crops (Frederick 1998, Anderson et al. 2016), and threats to native flora and fauna (Singer et al. 1984, Gabor and Hellgren 2000, Siemann et al. 2009, Jolley et al. 2010, Chapter 2). Thus there is a need to understand movements and behaviors of wild pigs in newly colonized areas. Assessing movement states not only represents a novel approach for understanding ecology of this invasive species but also provides information useful to eradication and control policies and activities.

We explored movement ecology of a low-density, emergent wild pig population in the state of Michigan, US. Specifically, we: *i*) assigned movement states to wild pig locations derived from GPS telemetry collars, *ii*) correlated landscape composition, structure, and weather variables with movement states, and *iii*) predicted likelihood of movement states given a range of biotic and abiotic conditions. Our study represents a novel approach for exploring movements in wild pigs, and provides much needed information on the ecology of this species in newly-colonized northern systems.

3.3 Methods

3.3.1 *Study Area*

Our study area included portions of six counties (Arenac, Bay, Gladwin, Midland, Ogemaw, and Roscommon) in the central Lower Peninsula and one county (Marquette) in the western Upper Peninsula of Michigan (Fig. 3.1). I selected these counties based on wild pig reports received by the Michigan Department of Natural Resources (MDNR) and United States Department of Agriculture - Wildlife Services. Wild pig populations in Michigan have broadly been classified as emerging to transitional (Mayer 2009), with populations characterized as low-density (unpublished data USDA-APHIS). Climate in this study area is characterized by humid summers and cold winters. Average monthly temperatures for counties in the Lower Peninsula range from -6.5 (January) to 20.8 ˚C (July) with average monthly precipitation highest in September (8.9 cm) and lowest in February (3.9 cm; Michigan State Climatologist's Office 2019). In Marquette County, average monthly temperatures range from -9.9 (January) to 18.5 ˚C (July) with average monthly precipitation highest in October (9.8 cm) and lowest in February (5.4 cm; Michigan State Climatologist’s Office 2019). Study area counties in the Lower Peninsula fall along a forest transitional zone, comprised primarily of deciduous hardwoods in the south and conifer, mixed conifer, and hardwoods in the north (Barnes and Wagner 1981, Albert 1995). Coarsely, land cover in this region is primarily agriculture and forestlands with interspersed woody and emergent wetlands throughout. Marquette County is evenly divided by a regional landscape boundary, with the eastern portion being mostly forested and broadly characterized by lowlands with swamps and bogs often dominated by conifers (Barnes and Wagner 1981, Albert 1995). The western portion of Marquette County is also mostly forested and consists of northern hardwoods, though conifers may be locally dominant (Barnes and Wagner 1981, Albert 1995).

3.3.2 *Capture and Handling*

From 2014 to 2017, I live-captured wild pigs using a combination of neck snaring and corral traps (1.5 m tall metal fencing with a guillotine door) baited with soured corn. Captured animals were immobilized using a combination of xylazine (Rompun®, Miles Inc., Shawnee Mission, Kansas, USA) and Telazol (Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA). Animals were equipped with IridiumTrackM collars (Lotek Wireless Inc., Newmarket, Ontario, Canada) programmed to record a GPS-fix every 30 minutes. Due to the unique morphology of wild pigs, I fashioned a harness that attached to the collar and behind the front legs to help secure the collar to the animal. Capture and handling protocols were approved by the Michigan State University Institutional Animal Care and Use Committee (01/14-013-00).

The duration that collared individuals transmitted data varied due to harvest of animals by hunters and collar malfunctions. The MDNR declared wild pigs an invasive species in 2013 allowing for indiscriminate harvest of this species by the public, which ultimately led to removal of several individuals under study. For these analyses, GPS data were from individuals that carried active collars for at least three months.

3.3.3 *Movement State Metrics*

To quantify wild pig movement states I considered movement trajectories and time-use in local convex hulls. I chose these outputs because they incorporated aspects of movement and space use readily linked to behavior and ecology. I calculated metrics from these outputs separately for individuals in this analysis. Prior to calculating metrics, I removed locations of poor quality (i.e., having a dilution of precision (DOP) >5). I also removed the first seven days of tracking following collaring of each animal. I did so to eliminate any biased movements associated with post-capture stress. I used the adehabitatLT package in program R (version 3.5.0) to calculate movement metrics for each trajectory (Calenge 2011). A trajectory is defined as multiple discrete steps that connect sequential relocations of an animal (Turchin 1998). From trajectories, I extracted step-lengths (distance between successive locations; SL), which indicate rate of movement and represent a common metric used in assigning movement states (Franke et al. 2004, Morales et al. 2004). Since trajectories are time-sensitive, I specified a new trajectory *post-hoc* if successive locations were >32 or <28 minutes apart. This prevented calculation of abnormally large or small step-lengths in a trajectory due to irregular GPS-fixes.

Next, to delineate local hulls I used the T-LoCoH package (Lyons 2014) in R to create home ranges for each individual. The T-LoCoH method is unique in that it incorporates time stamps to calculate time-scaled distances used in local convex hull estimation (Lyons et al. 2013). In essence, this method provides a temporally-explicit estimate of a home range and allows for calculation of time-use metrics in local hulls, such as revisitation rate (number of separate visits to a location over time; NSV) and duration of visit (mean number of locations per visit; MNLV; Lyons et al. 2013). In calculating hulls, I selected the *a*-method for nearest neighbor generation that uses a cumulative distance and is optimal for estimating conservative hulls robust to overestimation (Lyons 2014). Calculation of time-use metrics are contingent upon an inter-visit gap (IVG), which specifies the amount of time an animal would need to be away from a hull for calculations of time-use metrics to be re-initiated. I selected a temporally resolute IVG (i.e., one hour), because I was primarily interested in movements and behaviors at fine temporal scales.

3.3.4 *Identifying Movement States*

I conducted k-means clustering on three movement metrics (SL, NSV, and MNLV) using the optimal number of clusters (i.e., movement states) specified by the gap statistic (Tibshirani et al. 2001). Use of k-means to identify movement states has been implemented and suggested as a viable tool for exploring animal movements and behaviors (Van Moorter et al. 2010). I used the gap statistic method to estimate optimal number of clusters (k), which compares variation within clusters for different values of k (Tibshirani et al. 2001). To do this, I used the clusGap function in the cluster R package (Maechler et al. 2012). I specified a maximum of 10 potential clusters and used 1000 bootstrap replicates to identify optimal number of clusters. I selected a maximum of 10 potential clusters to remain consistent with other large ungulate movement studies (Van Moorter et al. 2010), and delineation of >10 movement states becomes difficult to describe behaviorally. Optimal number of clusters was specified as the instance where the gap statistic was maximized (Tibshirani et al. 2001).

3.3.5 *Habitat and Weather Covariates*

Next, I developed a database of habitat and weather covariates found to influence wild pig movements, behaviors, and ecology (see Table 3.1). I was interested in associations between wild pig movement states and proportions of land cover types tall enough to provide overhead cover or forage for wild pigs. Thus, I extracted variables from existing vegetation type and height rasters (30-m resolution) provided by the 2014 LANDFIRE Program (LANFIRE EVT, LANDFIRE EHT; http://www.landfire.gov/). Then I overlaid a grid at a resolution of 100 m, corresponding to the average distance moved between subsequent GPS locations by individuals in this study ($\bar{\bar{x}}$ = 100 m, SE = 1.37). Within each grid cell, I calculated proportion of area that was developed, riparian, emergent marsh/herbaceous open, or hard mast cover (Table 3.1). I reclassified the LANDFIRE EHT vegetation height raster into two classes: open areas and high vegetation (>5 m), as this allowed me to delineate edge between open and closed cover types (Table 3.1). Additionally, I reclassified the LANDFIRE EVT raster for agriculture and high shrub cover (>3 m in height), to calculate patch cohesion (Table 3.1). I used the spatialEco package (Evans 2015) in R to calculate open-forest edge density (ED) and patch cohesion indices for reclassified agriculture and shrub layers (PCI) within each cell of this grid (Table 3.1).

I obtained weather data from the National Oceanic and Atmospheric Administration (NOAA) online portal. I extracted hourly data from three local weather stations (Gwinn, Saginaw, and Roscommon), matching the temporal extent of wild pig GPS data used in this analysis. I appended data from the closest weather station to each location at a resolution of the nearest hour. Here, I considered surface pressure (Pa) and ambient temperature (˚C; Table 3.1).

3.3.6 *Modeling*

Using movement state as the response variable (with number of levels specified by the gap statistic method for optimal clustering), I fit mixed multinomial logistic regression models in R and STAN (Carpenter et al. 2016) via the brms package (Bürkner 2017). I used a Bayesian framework with a static Hamiltonian Monte-Carlo Sampler that allowed for inclusion of random effects (Duane et al. 1987, Neal 2011). I tested for multi-collinearity by calculating variance inflation factors for all covariates within the model, where any covariate with a value > 3.0 was removed (Zuur et al. 2010). In addition, I standardized each predictor variable to have a mean of 0 and standard deviation of 1. The model estimating movement state took the form:

$$\mathrm{P}(Yi = K - 1) = \frac{e^{\beta_{K-1}{}^{*}x_i}}{1 + \sum \frac{K - 1}{k = 1}\, e^{\beta_{k}{}^{*}x_i}}$$

Where *Yi* is the response variable, *K* is possible outcomes, β are regression coefficients, and *Xi* is a vector of fixed and random effects for a particular outcome (*k*). I took a two-step approach to modeling. First, I fit an intercept only model to serve as a null or baseline for model comparisons. Next, I fit a model incorporating random effects for individual wild pig, year, and cohort. Here, cohort represents an identifier attached to individuals captured together and considered to be in the same social group. Models were ranked using leave-one-out cross-validation information criterion (LOOIC; Vehtari et al. 2017), a preferred method to deviance information criterion (DIC) and widely-applicable information criterion (WAIC; Gelman et al. 2014). I retained the model with lowest LOOIC for fitting of a fully parameterized model.

I specified non-informative priors and ran 3 chains of 5000 iterations with a burn-in of 1000 and thinned each chain by 10. Convergence was assessed via visual inspection of trace and density plots and further evaluated for each parameter by R-hat value < 1.1 (Gelman and Hill 2006). I deemed a parameter to be significant if 95% credible intervals did not overlap 0. Predictions were generated for each significant parameter and estimated across the range of an isolated variable while holding all other predictors at their mean. To test predictive performance of this model, I subset GPS data into training and testing sets. I trained the model using 80% of GPS locations, randomly selected from each individual. The remaining 20% of data were used to test the model and estimate classification accuracy using a one-vs-rest approach (Anand et al. 1995) that allowed independent estimation of area under the receiver operating characteristic curve (AUC; Hanley and McNeil 1982) for each level in multi-level response models. Values of AUC range from 0.0 to 1.00 where those closer to 1.00 indicate near perfect predictive performance.

3.4 Results

From 2014 to 2018, I collared 8 wild pigs (2-M, 6-F) from my study area in the Lower Peninsula and 2 (2-F) from the Upper Peninsula. Fix rates for collars were relatively high at ~98% across all individuals with mean DOP of 3.14 (SE = 0.01). After data cleaning, I used 39,915 locations to generate movement trajectories, local convex hulls, and determine optimal number of clusters. Mean number of locations per individual was 3,992 (SE = 993) with seasonal representation being highest in fall (September ─ November) and lowest in summer (June ─ August; Table 3.2).

Our optimal clustering analysis revealed three clusters (movement states; Fig. 3.2). Using k-means to assign each location a cluster grouping, I characterized each state using descriptive statistics related to SL, NSV, and MNLV (Table 3.3). Rapid movement – low fidelity (RM-LF) behaviors included relatively large movements, moderate revisitation (pigs often used similar travel routes), and low visit duration (Table 3.3). This state may correspond to directed travel of fleeing behaviors in wild pigs. Moderate movement – high fidelity (MM-HF) behaviors included intermediate step lengths, lowest revisitation, and high visit duration (Table 3.3). The MM-HF state aligns with resting and other sedentary activities. Low movement – moderate fidelity (LM-MF) behaviors included smallest step lengths and highest revisitation rates, along with intermediate duration of visit (Table 3.3). This state may be indicative of foraging and exploratory behaviors. Given that wild pigs are primarily nocturnal, I further investigated movement states by time of day. Consistent with expected behaviors, I found more active states (relocating and foraging) at night, and resting during the daytime (Fig. 3.3).

3.4.1 *Modeling*

I found that the model including random effects for individual pig, year, and cohort (LOOIC = 58213.4, weight = 1.00) outperformed the null model (LOOIC = 65471.5, weight = 0.0). Variance inflation factors for all 10 predictor variables were <3.0, indicating lack of multicollinearity. Trace and density plots indicated that each model chain effectively explored parameter space and converged. In addition, all predictor variables converged in the full model as indicated by R-hats being <1.1.

Compared to RM-LF, several predictor variables significantly influenced the probability of a wild pig being in LM-MF or MM-HF movement states (Table 3.4). I found that probability of RM-LF increased as proportion human development and hard mast increased (Fig. 3.4a,b). The effect size for RM-LF was most pronounced for amount of human development, where probability of RM-LF increased exponentially and peaked at ~0.90 as proportion of human development increased (Fig. 3.4a). I also found that probability of RM-LF linearly decreased as riparian cover type increased, but LM-MF and MM-HF increased in these areas (Fig. 3.4c). Similarly, amount of emergent marsh/herbaceous open was negatively related to RM-LF, while probability of MM-HF increased (Fig. 3.4d). Emergent marsh/herbaceous openings had minimal effect on LM-MF (Fig. 3.4d).

Our landscape metrics also proved influential in predicting wild pig movement states (Table 3.4). I found a large effect size for foraging and patch cohesion index for agriculture, with likelihood of LM-MF increasing as cohesion of agricultural patches increased (Fig. 3.5a). The probability of RM-LF and MM-HF tended to decrease with increasing agricultural patch cohesion (Fig. 3.5a). For shrub cover types, probability of MM-HF increased as patch cohesion increased, while LM-MF and RM-LF decreased (Fig. 3.5b). Lastly, I found that wild pigs used areas with more open to forest edge during LM-MF states, but the effect size was minimal (Fig. 3.5c).

Weather variables significantly related to wild pig movement states (Table 3.4). I found that probability of LM-MF decreased as temperatures increased, and that MM-HF and RM-LF increased with increasing temperature (Fig. 3.6a). Increasing surface pressure corresponded to higher probabilities of LM-MF state and less RM-LF, with minimal effect on MM-HF (Fig. 3.6b). I failed to find a strong effect of Julian date on wild pig movement states (Fig. 3.6c). Given the small effect sizes of Julian date I suspect that interaction results were spurious (Table 3.4).

I found that models performed better than random (i.e., AUC's >0.5), and that the ability to predict RM-LF state was highest (AUC = 0.69; Fig. 3.7c), followed by MM-HF (AUC = 0.65; Fig. 3.7a) and finally, LM-MF (AUC = 0.62; Fig. 3.7b). I applied my model to the full study area extent and smoothed the output using bilinear interpolation at 30 m resolution (Figs. 3.8-3.10). Predicted probabilities of wild pig movement states ranged from 0 to 1 for both MM-HF and RM-LF states (Figs. 3.8, 3.10) but were slightly lower for LM-MF states (0-0.50; Fig. 3.9)

3.5 Discussion

Movement remains an understudied aspect of wild pig ecology. Interpretation of movement data hold great promise for documenting space use of this invasive species. My delineation of three movement states of wild pigs, classified as MM-HF, LM-MF, and RM-LF, revealed that wild pig movement states can effectively be assigned using movement trajectories and local time-use metrics. In addition, I found that aspects of landscape cover types, structure, and weather influenced wild pig movement states. I observed a positive influence of development and hard mast cover types on probability of RM-LF. I also discovered that increasing riparian cover type corresponded to increases in probability of LM-MF and MM-HF. For landscape structure, cohesive areas of agriculture and shrub cover types corresponded to increased LM-MF and MM-HF, respectively. I also found that probability of LM-MF decreased with increasing temperatures. These findings provide information on biotic and abiotic conditions that influence behavior and movement ecology of wild pigs.

Exploring influence of cover type on species movements and behaviors is a common theme in wildlife research (Zeller et al. 2012), as it often reveals important patterns in animal-habitat associations that can improve ecological understanding. In developed areas, I found that wild pigs were likely in the RM-LF state, consistent with previous studies indicating that wild pigs are cryptic and adjust activities and movements to avoid humans (Saunders and Kay 1991, Wyckoff et al. 2012, Podgórski et al. 2013). The negative relationship between LM-MF state and hard mast amount was unexpected, as I hypothesized that this cover type would be important for associated behaviors such as foraging given prevalence of hard mast (e.g., acorns, hickory nuts, and beechnuts) in wild pig diets (Fournier-Chambrillon et al. 1995, Schley and Roper 2003, Schlichting et al. 2015), especially in fall and winter months when aboveground forage is scarce. I recognize that cover type by itself is likely a poor indicator of mast production, as production varies substantially across species and years (Gysel 1971, Kelly 1994, Koenig and Knops 2000). During the four years of my study, acorns were particularly abundant for at least one year. Collared pigs undoubtedly foraged in mast producing cover types during and after this period of abundant acorns, as evidenced by telemetry locations and corresponding areas of rooting, yet the behavior was highly ephemeral, likely corresponding to acorn abundance (Schlichting et al.

2015). I proffer that rather than a relationship to mast production, increasing RM-LF and decreasing LM-MF more likely related to lack of understory vegetation (and thus concealment) provided by mature forests of this cover type.

Movement states that I observed for areas with relatively high amounts of riparian and emergent marsh/herbaceous open were likely related to thermoregulatory and security behaviors of wild pigs. These cover types offered dense visual cover and thermoregulatory refuge (Caley 1997, Mersinger and Silvy 2007, Cooper and Sieckenius 2016). Furthermore, use of riparian habitats for foraging is consistent with study results from other parts of the U.S. (Wood and Roark 1980, Arrington et al. 1999, Zengel and Conner 2008) and abroad (Dardaillon 1987, Cahill et al. 2003). Similarly, increased probability of MM-HF in emergent marsh/ herbaceous open cover types aligns with areas that contain standing water for resting, wallowing, and aiding in thermoregulation during warmer temperatures (Wood and Brenneman 1980, Barrett and Birmingham 1994). In addition, thick and contiguous vegetation for cover was an important component of wild pig space use in my study, corresponding to MM-HF state in areas with higher shrub patch cohesion (see also Gaston et al. 2008), especially in winter (Dexter 1998).

Most investigations into influences of landscape structure on wild pig movements relate to agricultural damage juxtaposed to forest edge, where proximity to forest edge increases likelihood of damage and use by wild pigs (Gerard et al. 1991, Meriggi and Sacchi 2001, Thurfjell et al. 2009). I found a relatively minor influence of open to forest edge density on all movement states. Conversely, patch cohesion of agriculture and shrub cover types was more influential of wild pig movement state. Given that most agriculture fields in my study area were >1 ha, the positive influence of agricultural patch cohesion on probability of LM-MF suggests that this may align with foraging behavior and is more likely to occur in large, contiguous interiors of agricultural fields. This differs from Sweden where wild pig damage occurred near forest edges and at the periphery of agricultural fields, though this effect was reduced when crops were mature (Thurfjell et al. 2009). Wild pigs in my study used mature corn for both resting cover and forage (Łabudzki et al. 2009, Thurfjell et al. 2009, Morelle and Lejeune 2015). To my knowledge, this is the first investigation of wild pig movements related to landscape metrics in the U.S., and these findings merit consideration of these features in future movement research on wild pigs.

Impacts of weather on wild pigs has been explored in the southern U.S., broadly indicating that increasing temperature and pressure lead to a corresponding decrease in movements at multiple scales, though this relationship was not always linear (Kay et al. 2017). Others also noted reductions in wild pig activity coinciding with increasing temperature (Blasetti et al. 1988, Lemel et al. 2003, Wyckoff et al. 2006). My findings on temperature effects are consistent with these studies, as I observed a linear decrease in probability of LM-MF state, representative of foraging and exploratory behaviors (i.e., decrease in activity), with increasing temperatures. While not as pronounced, I also observed that wild pig LM-MF state increased with increasing pressure. Reduced movements in response to low pressure has been noted in other research exploring fine-scale movement in wild pigs, however, this relationship was quadratic indicating reduced movement at both high and low surface pressures (Kay et al. 2017). Behavioral and movement responses to changing pressure have been noted in several ungulate species (Malechek and Smith 1976, Webb et al. 2010), with some documenting increases in movement and activity with increasing pressure (Dussault et al. 2006). These behavioral changes may be driven by impending storms (Tilton and Willard 1982), as declining surface pressure is often indicative of inclement weather. However, I caution that pressure could have a lag effect on species responses, not effectively captured in my analysis. In addition, despite noted seasonality in wild pig movements and space use (Singer et al. 1981, Calenge et al. 2002, Lemel et al. 2003, Hayes et al. 2009, Kay et al. 2017), I observed minimal impacts of Julian date on probabilities of movement states. Similar levels of each movement state throughout the year could signify that, at least at fine spatio-temporal scales, wild pigs in northern systems of the US do not experience major seasonal fluctuations in movements like those observed in other geographic regions.

I caution that this study was based on a limited sample (i.e., 10 individuals), therefore, I encourage further exploration of wild pig movements in similar environments to elucidate potential geographic similarities and differences. In addition, I focused on impacts of cover types, landscape structure, and weather and thus my findings are inherently linked to the fine spatio-temporal scales I examined. Nevertheless, I believe the scales of this analysis are highly relevant to practitioners and managers, especially those faced with controlling localized and emerging populations of wild pigs. Quantification of wild pig movements, much like any other animal, is scale-dependent and patterns that I observed could change if evaluated at different spatio-temporal scales (Kay et al. 2017).

Our study is the first attempt to correlate wild pig movement states to fine-scale biotic and abiotic conditions, while providing further insights into the ecology, function, and management of this species in northern systems of the U.S. I believe this research offers two main contributions on the topic of wild pig ecology. First, as indicated by Morelle et al. (2014), wild pig movement is an understudied topic and there is a need to relate movement signatures to behavior to better understand ecology of this species. I found methods using k-means clustering along with attributes from movement trajectories and time-use metrics from local convex hulls to be an intuitive approach for delineating movement states in wild pigs from GPS data. Along with semi-hidden Markov models and other state-space modeling techniques, these methods offer another approach for assigning movement states to GPS data. Second, this study is one of the first to explore wild pig movements within northern systems of the US where pigs occur at low densities, likely contributing to movement patterns quantified herein.

3.6 Acknowledgements

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APPENDIX

Table 3.1.

Variable names, description, data source, mean, range, and references for covariates used in modeling movement states of 10 wild pigs GPS telemetry-tracked in Michigan, USA between 2014 and 2018.

Name	Description	Source[a]	$\bar{\bar{x}}$ (SE)	Range	Reference(s)
Proportion Cover Type					
Developed	Proportion of developed cover types in 1 ha cells	LANDFIRE	1.23 (0.03)	0.00 – 100.00	Ohashi et al. (2012), Podgórski et al. (2013), Gantchoff and Belant (2015)
Riparian	Proportion of eastern floodplain forest and Atlantic swamp forest cover types in 1 ha cells	LANDFIRE	39.79 (0.19)	0.00 – 100.00	Mersinger and Silvy (2007), Beasley et al. (2013), Cooper and Sieckenius (2016)
Emergent Marsh/Herbaceous Open	Proportion of open (i.e., transitional herbaceous, barren, quarries) and upland marsh (i.e., inland marshes and prairies) cover types in 1 ha cells	LANDFIRE	8.46 (0.10)	0.00 – 100.00	Wood and Brenneman (1980), Dardaillon (1987)
Hard Mast	Proportion of cover types dominated by mast producing tree species (i.e., white oak-red oak-	LANDFIRE	0.32 (0.02)	0.00 – 100.00	Singer et al. (1981), Bieber and Ruf (2005),

Table 3.1 (cont'd)

Name	Description	Source[a]	$\bar{\bar{x}}$ (SE)	Range	Reference(s)
	hickory, black oak and savanna, beech-maple-basswood) in 1 ha cells				Elston and Hewitt (2010)
Landscape Metrics					
Agriculture_PCI	Patch cohesion index (PCI) for row crop and close grown crop cover types	spatialEco/ LANDFIRE	0.39 (0.01)	0.00 – 4.44	Dardaillon (1987), Herrero et al. (2006), Morelle and Lejeune (2015)
Shrub_PCI	Patch cohesion index (PCI) for shrub cover types > 3 m	spatialEco/ LANDFIRE	0.26 (0.00)	0.00 – 4.31	Dexter (1998), Gaston et al. (2008)
Open-Forest Edge	Density of hard edge between open area and forest > 5 m	spatialEco/ LANDFIRE	2.10 (0.03)	0.00 – 26.00	Thurfjell et al. (2009), Morelle and Lejeune (2015)
Weather Metrics					
Temperature	Hourly temperature (˚C)	NOAA	5.26 (0.06)	-33.30 – 32.80	Dexter (1998), Schlichting et al. (2016), Kay et al. (2017)
Pressure	Hourly pressure (Pa)	NOAA	97,324.81 (3.89)	94,006.15 – 99,830.74	Kay et al. (2017)
Julian Date	Numeric representation of date to account for seasonality	-	199.40 (0.52)	1 – 365	Keuling et al. (2009), Podgórski et al. (2013)

Table 3.1 (cont'd)

[a] Source and/or method used to acquire data: spatialEco – landscape metrics calculated using the spatialEco package in program R (version 3.5.0); LANDFIRE – land cover and vegetation data from existing vegetation type and height rasters (30-m resolution) provided by the LANDFIRE Program (LANFIRE EVT, LANDFIRE EHT; http://www.landfire.gov/); NOAA – hourly weather data obtained from the National Oceanic and Atmospheric Administration.

Table 3.2.

Sex and number of GPS locations, by season, for 10 wild pigs tracked in Michigan, USA from 2014 to 2018.

ID	Sex	Fall[a]	Winter[a]	Spring[a]	Summer[a]	Total
F1	Female	2,565	2,234	165	661	5,625
F2	Female	1,957	0	0	0	1,957
F3	Female	0	79	40	0	119
F4	Female	0	1,054	38	0	1,092
F5	Female	0	1,371	3,327	2,441	7,139
F6	Female	1,080	0	1,007	0	2,087
F7	Female	2,655	3,820	0	0	6,475
F8	Female	2,929	2,162	2,273	2,603	9,967
M1	Male	2,762	0	0	0	2,762
M2	Male	2,692	0	0	0	2,692
Total		16,640	10,720	6,850	5,705	39,915

[a] Fall = September 1st – November 30th; Winter = December 1st – February 28th; Spring = March 1st – May 31st; Summer = June 1st – August 31st

Table 3.3.

Descriptive statistics of movement metrics for each movement state estimated for 10 wild pigs GPS telemetry-tracked in Michigan, USA from 2014-2018. SL = step-length in m; NSV = number of separate visits (revisitation); MNLV = mean number of locations per visit (duration).

	Movement State					
	Moderate Movement – High Fidelity		Low Movement – Moderate Fidelity		Rapid Movement – Low Fidelity	
Metric	$\bar{\bar{x}}$ (SE)	Range	$\bar{\bar{x}}$ (SE)	Range	$\bar{\bar{x}}$ (SE)	Range
SL	23.57 (0.86)	0 – 1,504	9.04 (0.06)	0 – 99	255.52 (2.87)	6 – 3,917
NSV	21.49 (0.17)	1 – 80	93.66 (0.36)	11 – 521	65.78 (0.55)	1 – 576
MNLV	11.14 (0.06)	2 – 52	5.97 (0.02)	2 – 16	4.05 (0.02)	1 – 20

Table 3.4.

Posterior means, standard error (SE), upper and lower 95% credible intervals for covariates in fully parameterized mixed multinomial logistic regression model for movement states of 10 wild pigs in Michigan, USA from 2014-2018.

Predictor	State[a]	Mean	SE	LCI 95%	UCI 95%
Proportion Cover Type					
Developed	**MM-HF**	**-0.15**	**0.02**	**-0.19**	**-0.11**
Riparian	**MM-HF**	**0.50**	**0.03**	**0.45**	**0.56**
Emergent Marsh/Herbaceous Open	**MM-HF**	**0.48**	**0.02**	**0.44**	**0.52**
Hard Mast	MM-HF	-0.04	0.02	-0.08	0.01
Developed	**LM-MF**	**-0.26**	**0.02**	**-0.29**	**-0.23**
Riparian	**LM-MF**	**0.46**	**0.02**	**0.42**	**0.50**
Emergent Marsh/Herbaceous Open	**LM-MF**	**0.27**	**0.02**	**0.23**	**0.31**
Hard Mast	**LM-MF**	**-0.05**	**0.02**	**-0.08**	**-0.02**
Landscape Metrics					
Agriculture_PCI	**MM-HF**	**-0.44**	**0.06**	**-0.55**	**-0.33**
Shrub_PCI	**MM-HF**	**0.29**	**0.02**	**0.26**	**0.34**
Open-Forest Edge	**MM-HF**	**-0.08**	**0.02**	**-0.12**	**-0.05**
Agriculture_PCI	**LM-MF**	**0.22**	**0.03**	**0.17**	**0.27**
Shrub_PCI	LM-MF	-0.01	0.02	-0.05	0.02
Open-Forest Edge	LM-MF	-0.03	0.01	-0.06	0.00
Weather Metrics					
Temperature	MM-HF	0.04	0.03	-0.01	0.09
Pressure	**MM-HF**	**-0.13**	**0.02**	**-0.17**	**-0.09**
Julian Date	MM-HF	-0.09	0.06	-0.20	0.03
Temperature	**LM-MF**	**-0.33**	**0.02**	**-0.36**	**-0.29**
Pressure	**LM-MF**	**0.04**	**0.02**	**0.01**	**0.07**
Julian Date	**LM-MF**	**-0.09**	**0.03**	**-0.16**	**-0.03**
Interactions					
Julian Date * Riparian	**MM-HF**	**-0.36**	**0.03**	**-0.41**	**-0.30**
Julian Date * Emergent Marsh/ Herbaceous Open	**MM-HF**	**-0.09**	**0.03**	**-0.13**	**-0.03**

Table 3.4. (cont'd)

Predictor	State[a]	Mean	SE	LCI 95%	UCI 95%
Julian Date * Hard Mast	**MM-HF**	**0.11**	**0.04**	**0.04**	**0.18**
Julian Date * Agriculture_PCI	**MM-HF**	**-0.34**	**0.08**	**-0.50**	**-0.17**
Julian Date * Shrub_PCI	MM-HF	-0.01	0.02	-0.06	0.03
Julian Date * Riparian	**LM-MF**	**-0.06**	**0.02**	**-0.11**	**-0.02**
Julian Date * Emergent Marsh/Herbaceous Open	**LM-MF**	**-0.20**	**0.02**	**-0.25**	**-0.15**
Julian Date * Hard Mast	LM-MF	0.02	0.02	-0.02	0.06
Julian Date * Agriculture_PCI	LM-MF	-0.04	0.04	-0.12	0.04
Julian Date * Shrub_PCI	**LM-MF**	**-0.05**	**0.02**	**-0.09**	**-0.01**

[a] MM-HF = moderate movement – high fidelity; LM-MF = low movement – moderate fidelity. All results relative to reference level of rapid movement – low fidelity (RM-LF).

Figure 3.1.

Seven county (Arenac, Bay, Gladwin, Marquette, Midland, Ogemaw, Roscommon) study area in Michigan, USA for the study of wild pig movement ecology.

Figure 3.2.

Optimal clustering of step-lengths, number of separate visits, and mean number of locations per visit using the gap statistic for 10 wild pigs in Michigan, USA from 2014–2018. Bars represent standard errors. Vertical dashed line indicates the gap statistic maximum.

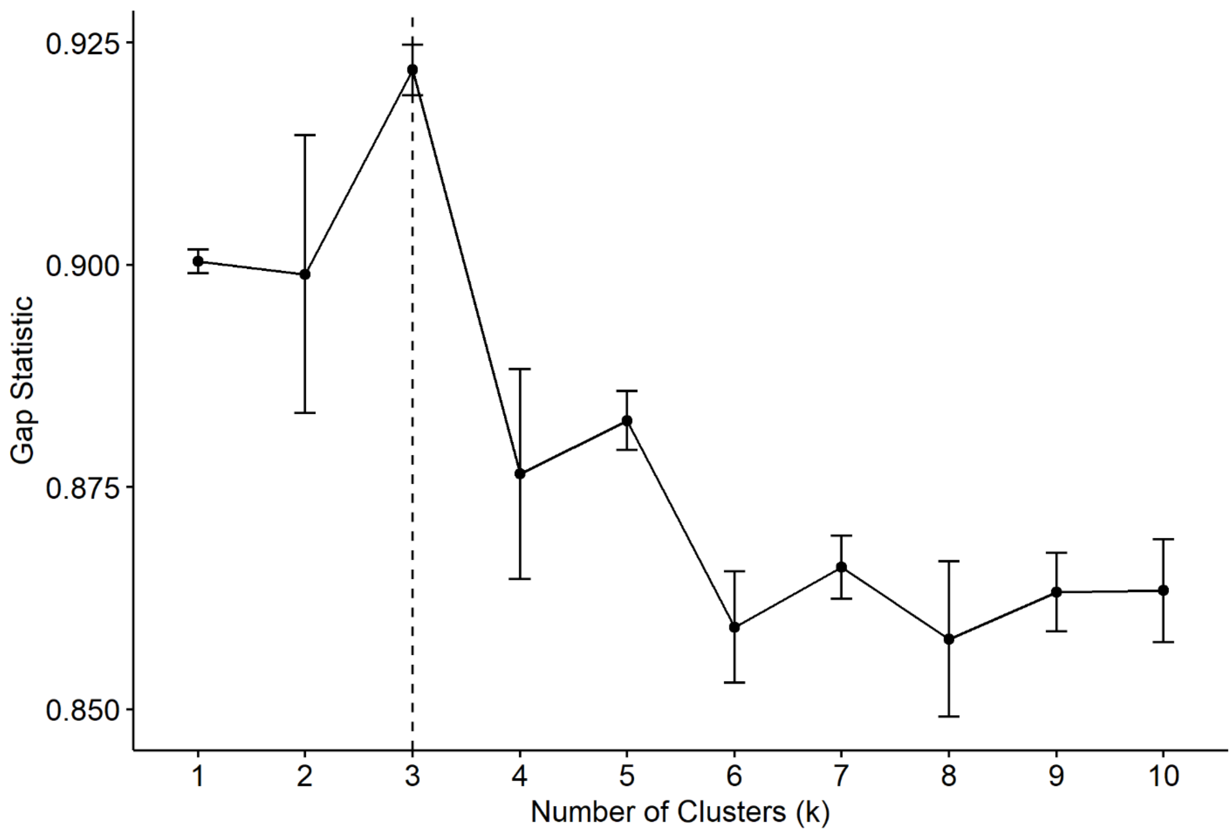


Figure 3.3.

Histogram of hourly frequency of a) moderate movement – high fidelity, b) low movement – moderate fidelity, and c) rapid movement – low fidelity observations.

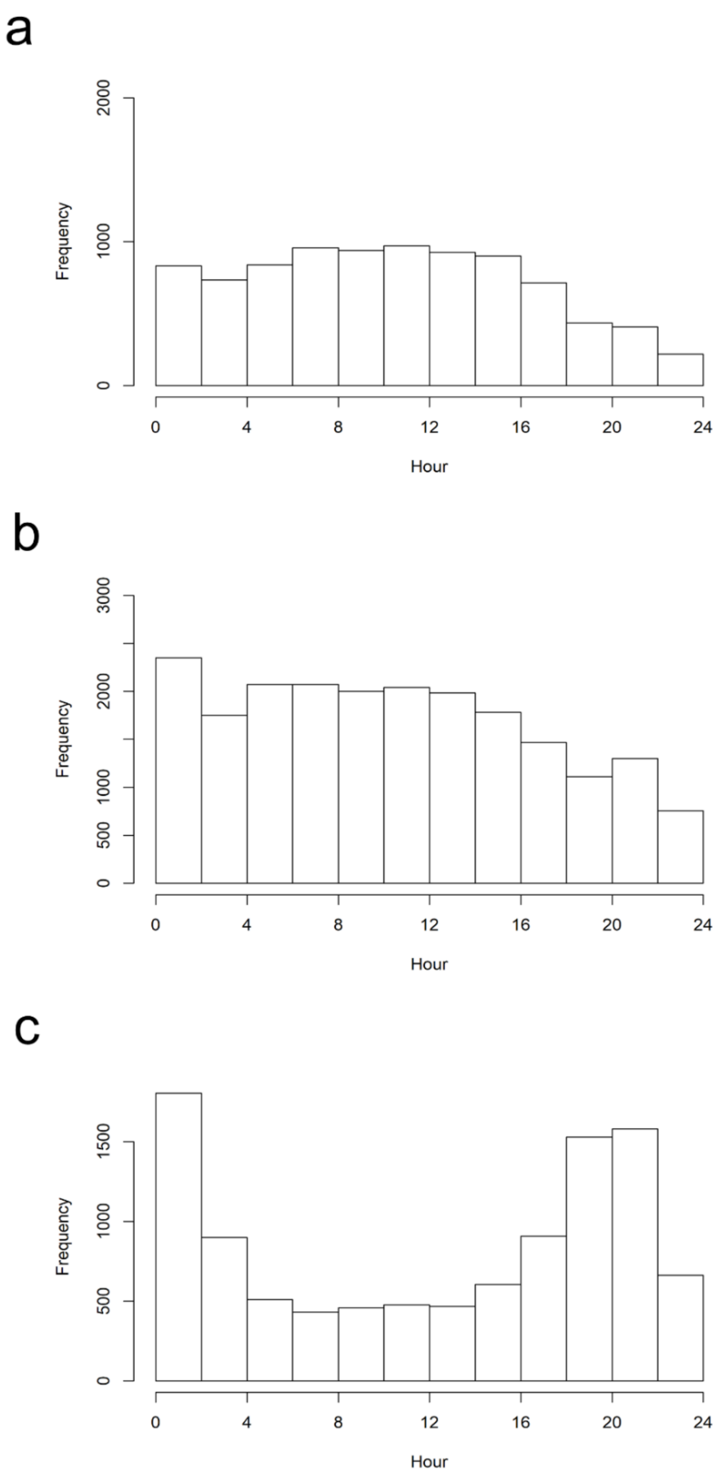


Figure 3.4.

Probability of movement state and proportion of a) developed, b) hard mast forest, c) riparian, and d) emergent marsh/herbaceous open cover types in 1 ha cells for 10 wild pigs in Michigan, USA from 2014-18. Shaded area represents the standard error of prediction estimates.

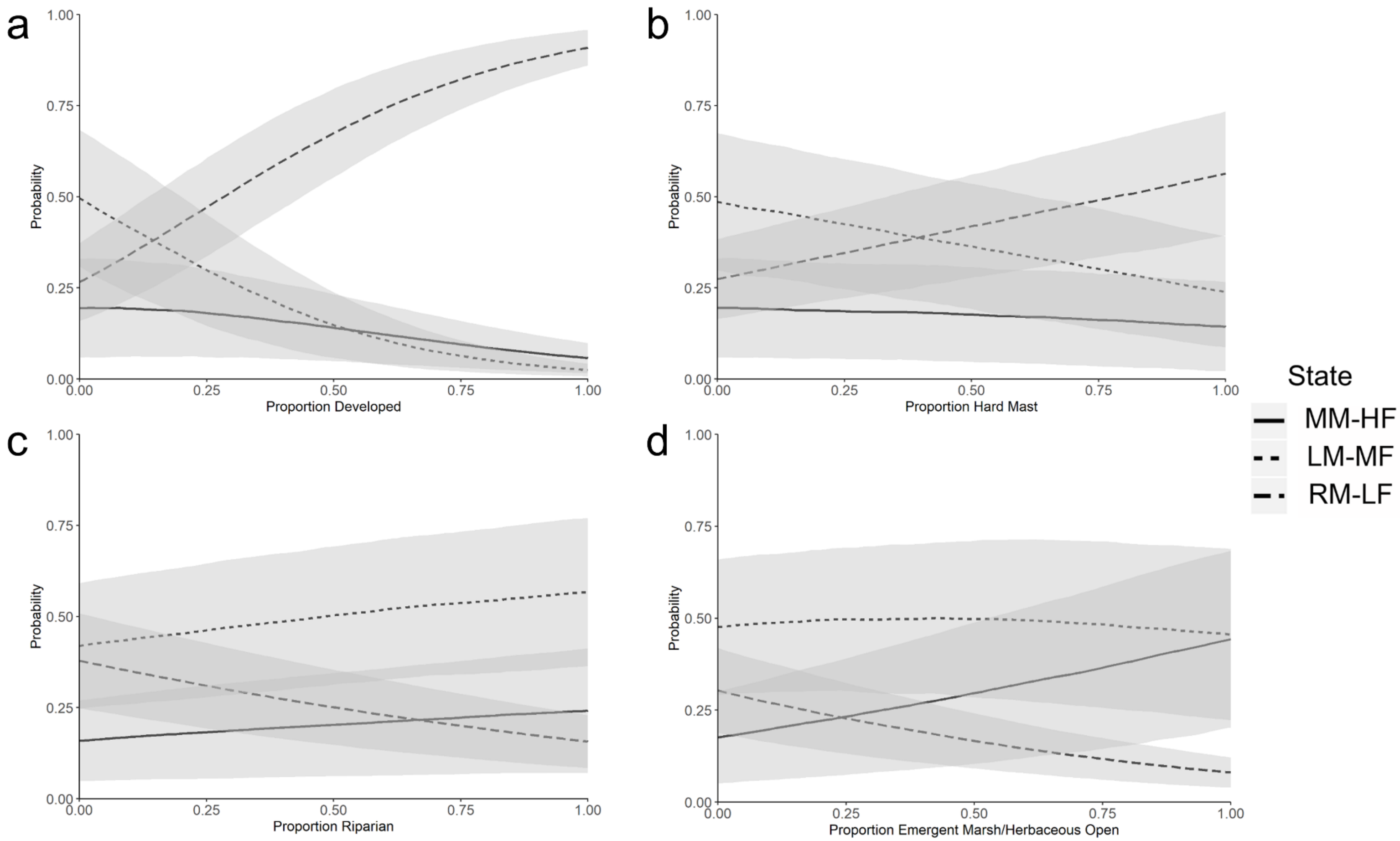


Figure 3.5.

Probability of movement state and landscape metrics: a) agriculture patch cohesion index, b) shrub patch cohesion index, and c) forest-open edge density in 1 ha cells for 10 wild pigs in Michigan USA, from 2014-18. Shaded area represents the standard error of prediction estimates.

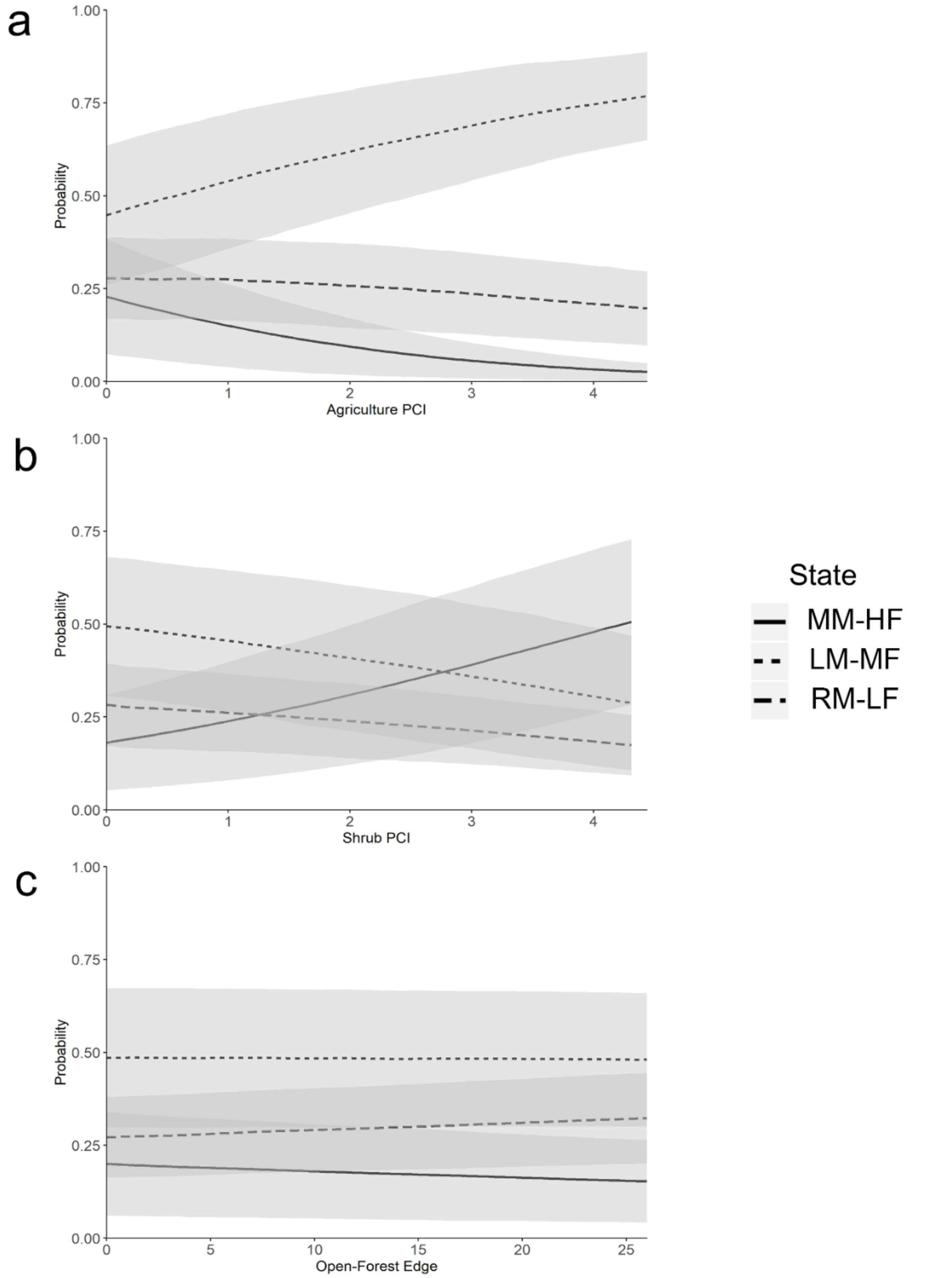


Figure 3.6.

Probability of movement state and climate metrics: a) temperature, b) pressure, and c) Julian date for 10 wild pigs in Michigan USA, from 2014-18. Shaded area represents the standard error of prediction estimates.

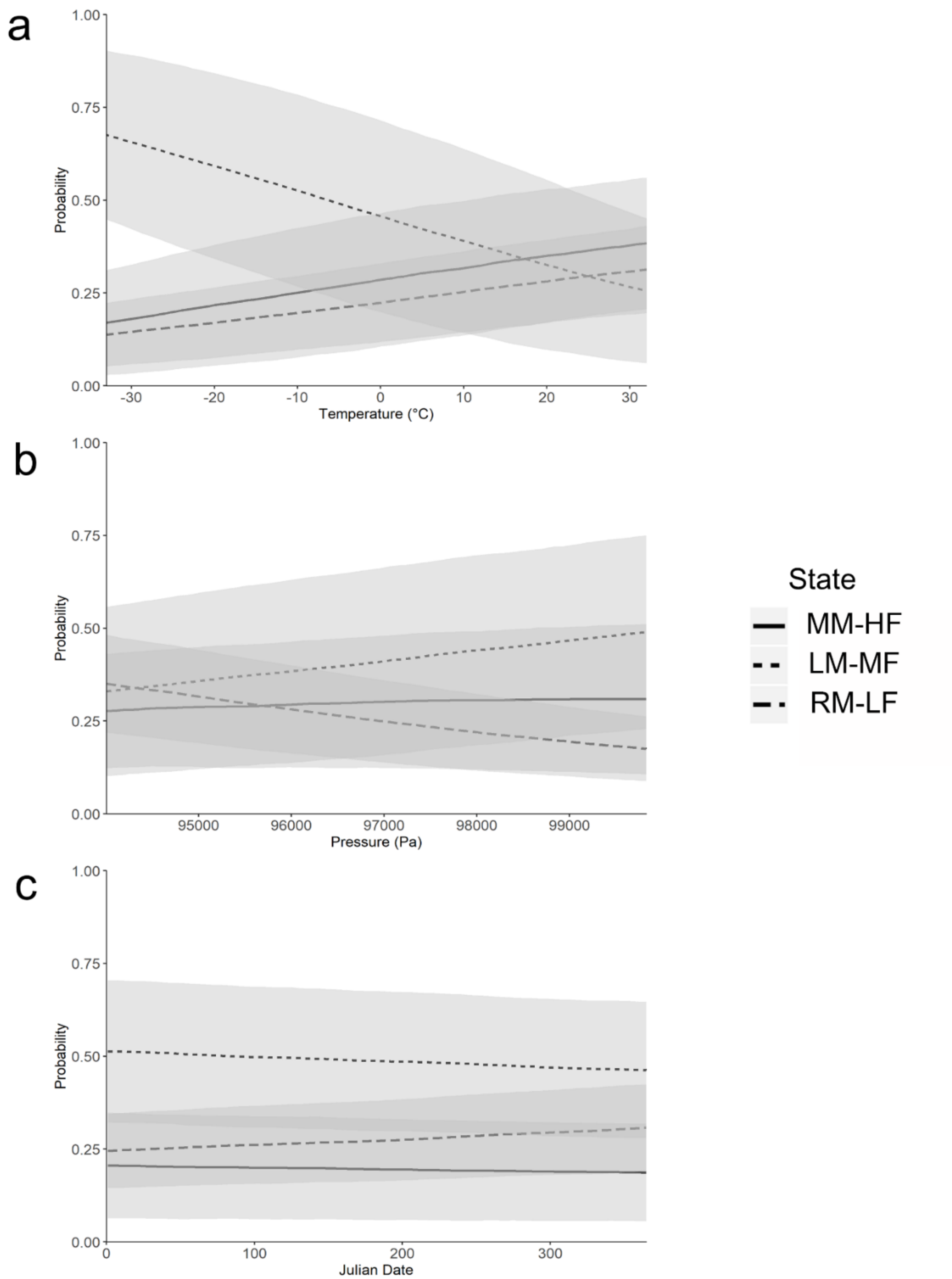


Figure 3.7.

Area under the receiver operating characteristic curve (AUC) for predictions of a) moderate movement – high fidelity, b) low movement – moderate fidelity, and c) rapid movement – low fidelity observations.

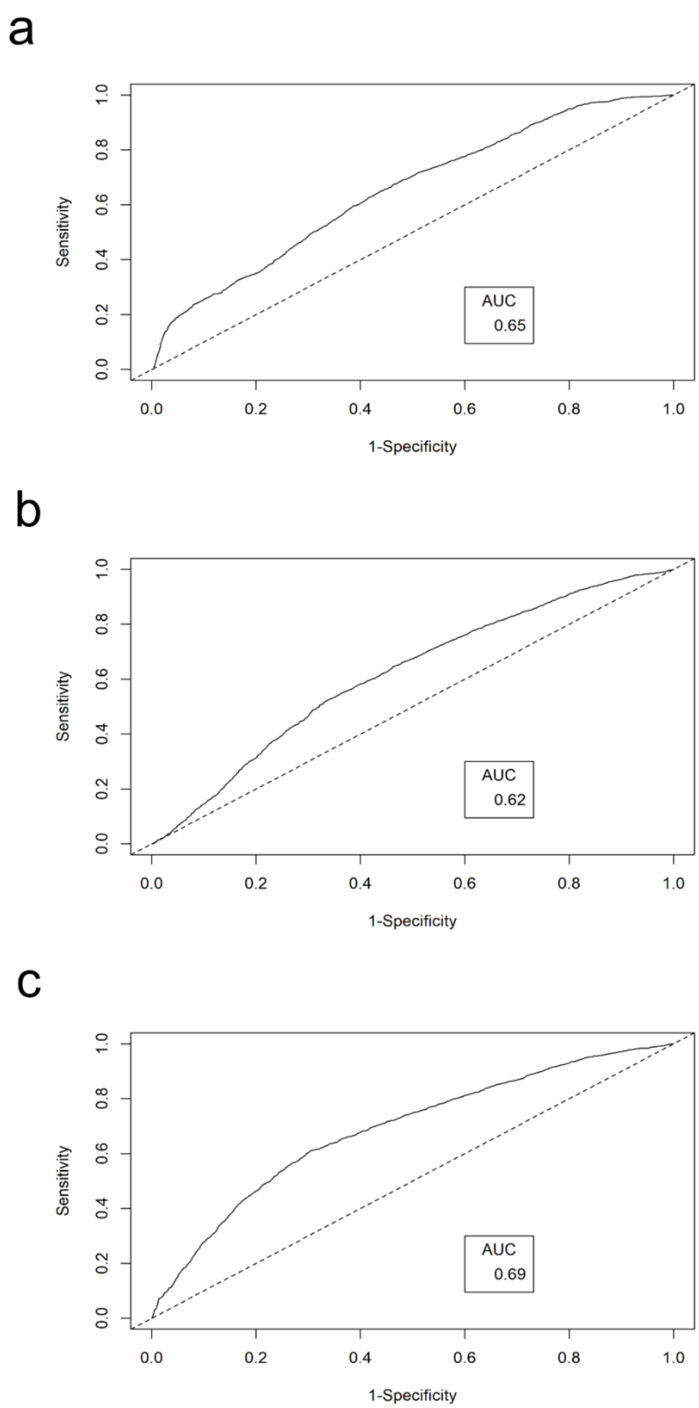


Figure 3.8.

Predictions of the probability of moderate movement – high fidelity state for wild pigs in Michigan, USA from 2014-2018.

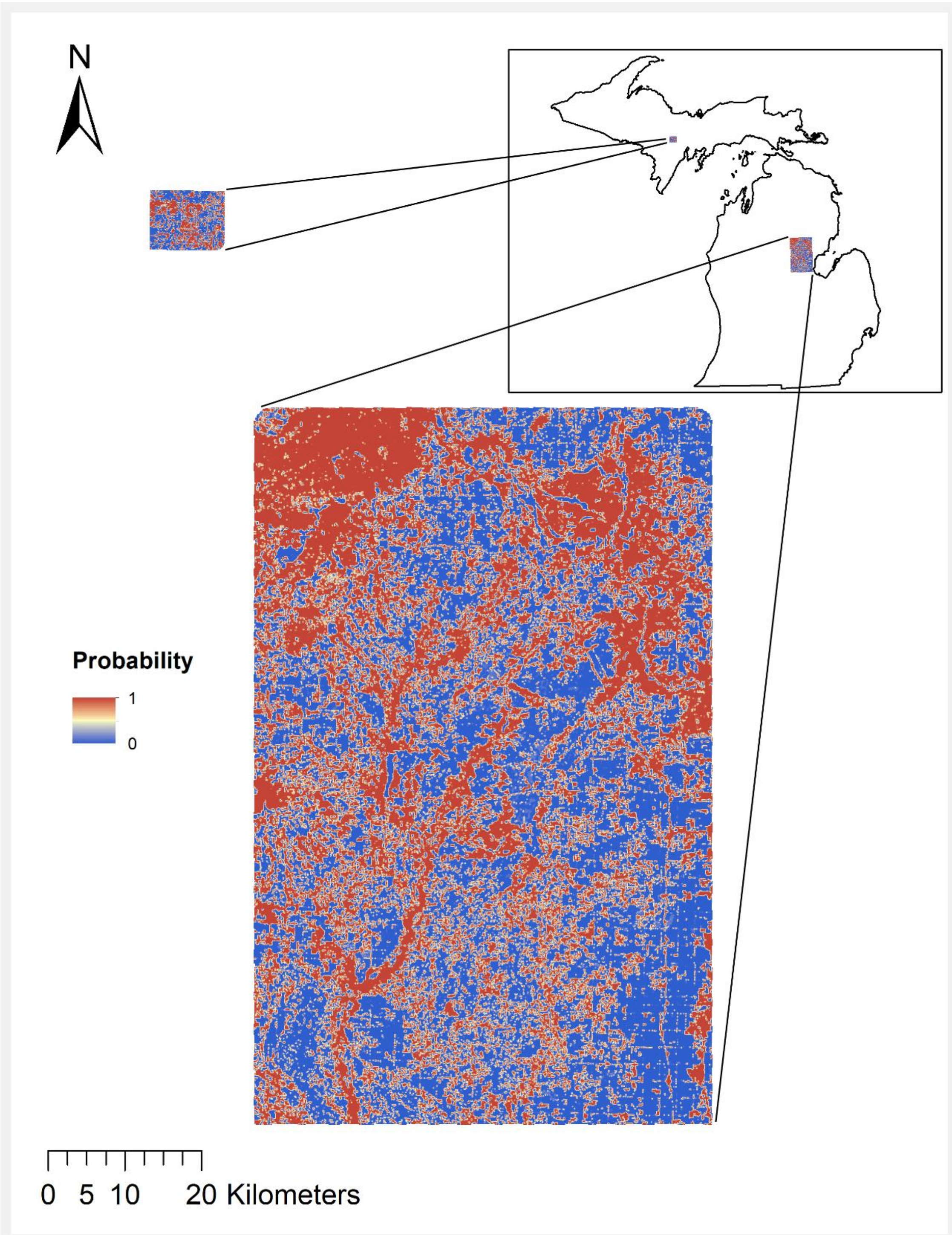


Figure 3.9.

Predictions of the probability of low movement – moderate fidelity state for wild pigs in Michigan, USA from 2014-2018.

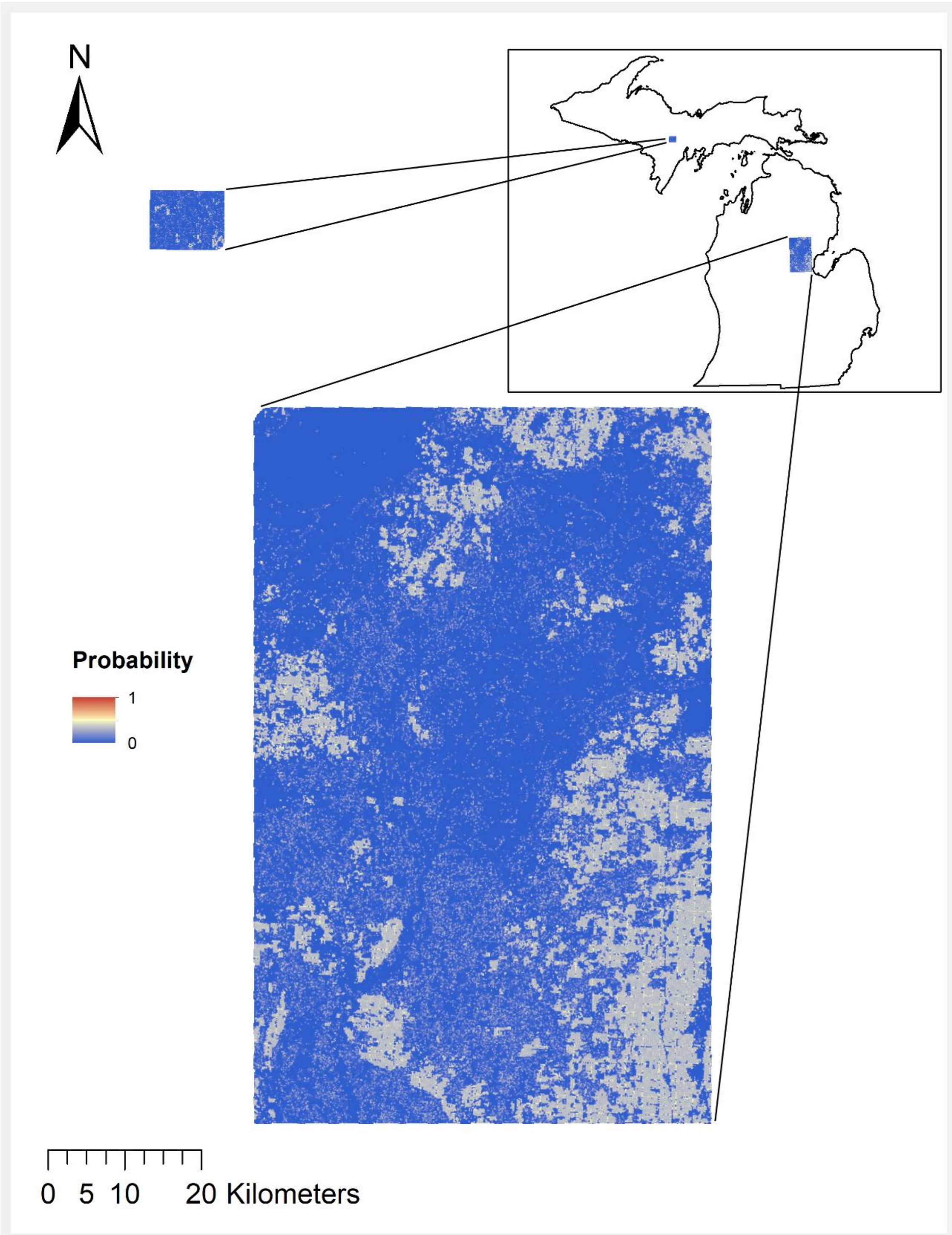
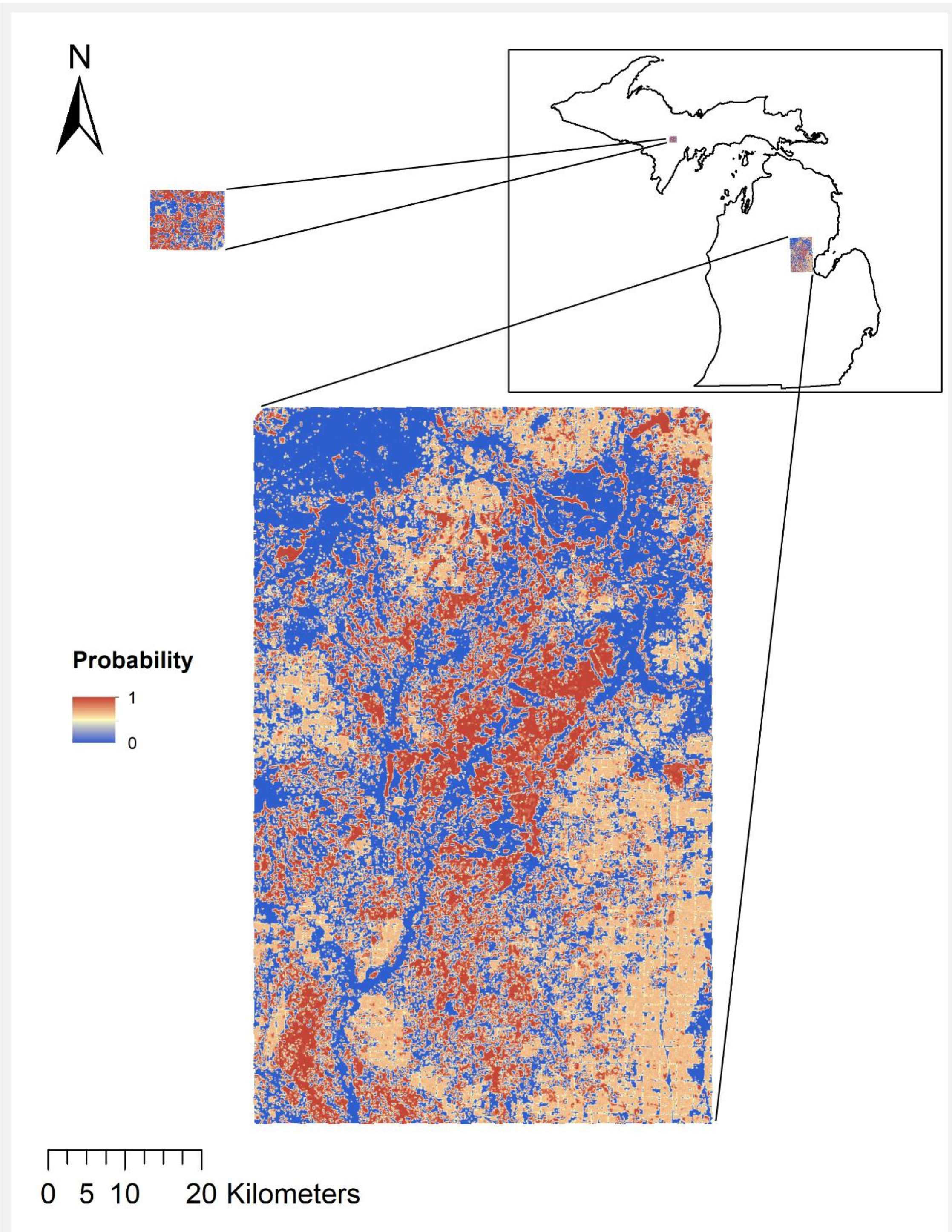


Figure 3.10.

Predictions of the probability of rapid movement – low fidelity for wild pigs in Michigan, USA from 2014-2018.



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CHAPTER 4:

SPATIO-TEMPORAL VARIATION IN AFRICAN LION ROARING IN RELATION TO A DOMINANCE SHIFT

We examined spatio-temporal patterns in African lion (*Panthera leo*) roaring in a reintroduced population before and after an apparent shift in the dominance hierarchy. Here, we mapped the configuration of lion roaring at the home range scale and quantified temporal signatures in roaring frequency using data collected during continuous follows during a 24-month period. Spatio-temporal patterns in roaring were closely tied to social hierarchy and shift in dominance that occurred within this population. We observed a distinct shift in roaring strategy, especially in the newly subordinate male coalition, which substantially reduced their roaring and altered space-use. Spatial configuration of subordinate male roaring also shifted from the periphery of their home range when they were dominant to the core of their home range. To view this article go to: https://doi.org/10.1093/jmammal/gyx020

CHAPTER 5:

THE RESEARCH-IMPLEMENTATION GAP LIMITS ACTIONABILITY OF HUMAN-CARNIVORE CONFLICT STUDIES

5.1 Abstract

Conflict with humans is one of the primary reasons why large carnivore populations are declining worldwide. Rates of human-carnivore conflict (HCC) are particularly high in East Africa, where human settlements tend to surround protected areas, maximizing potential for human-carnivore interactions. Despite extensive HCC research in this region, HCC persists, and carnivore populations continue to decline. Evident disconnects between HCC research and conservation action, management practices, and policy formation have been cited as mechanisms associated with these trends. I conducted a literature review to determine the extent to which HCC research in East Africa is actionable within the context of management and policy formation. I evaluated 36 papers for co-production, interdisciplinary collaboration, intent to inform management and policy, and stakeholder engagement. Many were published by co-authors in academia (63.8%) and collaborative efforts between academics and non-governmental organizations (25.0%), with limited representation outside of these sectors. Collaboration with disciplines outside of the natural sciences, specifically the social and political sciences (both 2.8%), was also uncommon although humans were the primary topic of study in 28% of papers. Moreover, while many papers were published in applied journals (86%), few explicitly stated policy and management objectives. Stakeholder engagement was mostly in the form of surveys and questionnaires rather than direct involvement in the research process. This review indicates

that HCC research currently lacks strong evidence of actionability and I provide recommendations for improving the practical salience of conservation research.

5.2 Introduction

Divides between research and policy can hinder efforts to derive practical benefits from scientific findings. Disconnects like these exist across disciplines and are evident in the fields of human health (Le May et al. 1998, Haines et al. 2004), psychology (Morrissey et al. 1997, Wandersman et al. 2008, Dimoff and Kelloway 2013), education (Abbott et al. 1999, Greenwood and Abbott 2001, Harvey and Kamvounias 2008, Cook and Odom 2013), business (Rho et al. 2001, Lilien et al. 2002, Tucker and Lowe 2014), and the natural sciences (Ehrlich and Kinne 1997, Opdam et al. 2001, Higgs 2005, McNie 2007, Shanley and López 2009). Probable causes for this disconnect include difficulties applying specific research findings to highly complex social, political, and ecological contexts, and professional distance that often exists between researchers and decision-makers (Knight et al. 2008). The research/policy divide is particularly problematic in the conservation sciences. Here, the 'research-implementation gap,' as it is commonly called, complicates efforts to avert species extinctions, trophic system disruption, and landscape change (Pfeffer and Sutton 1999, Opdam et al. 2001, Anonymous 2007, Born et al. 2009, Sunderland et al. 2009). For example, over half of 31 species of large carnivores remaining on the planet have populations that are declining (Ripple et al. 2014). There are many factors associated with these declines (see Macdonald 2016), but conflict with humans is among the most prominent (Woodroffe and Ginsberg 1998, Ripple et al. 2014). Thus, human-carnivore conflict (HCC) is one area in which implementation of conservation science is imperative if numerous large carnivore species are to be protected from extinction.

Conflicts that occur between humans and carnivores take many forms but typically involve competition over livestock. Livestock can be an easy target for carnivores given that they are less vigilant than wild prey (Kruuk 1972, Polisar et al. 2003, Kluever et al. 2008, Garcia et al. 2016) and often are easily accessible (i.e., herded into livestock enclosures or readily available on the grazing landscapes; Sillero-Zubiri and Laurenson 2001, Ogada et al. 2003, Woodroffe et al. 2007, Mwakatobe et al. 2013). Depredation of livestock can result in severe economic losses for affected individuals as livestock are an important contributor to economic well-being, particularly in developing nations (Patterson et al. 2004, Graham et al. 2005, Thirgood et al. 2005, Berger 2006, Holmern et al. 2007). In response to these livestock losses, affected humans may retaliate by killing or maiming carnivores perceived to be responsible (Graham et al. 2005, Thirgood et al. 2005, Kolowski and Holekamp 2006, Kissui 2008, Inskip and Zimmermann 2009). As a result, HCC is a leading cause of the global decline in large carnivore populations (Woodroffe and Ginsberg 1998, Woodroffe et al. 2005, Ripple et al. 2014). Thus, there is great need for management practices and policies capable of mitigating HCC for the benefit of conservation and human well-being alike (Treves and Karanth 2003, Inskip and Zimmermann 2009, Miller 2015).

In East Africa, rates of HCC are particularly high (Dickman et al. 2014, Ripple et al. 2014) due to presence of numerous carnivore species in and around protected reserves (Mills et al. 2001) and proximity of these reserves to human populations whose livestock are susceptible to depredation (Harcourt et al. 2001). For these reasons, East Africa has been a focus of HCC research (Montgomery et al. 2018). However, despite this research, populations of many carnivore species continue to decline, and high rates of HCC persist (Di Marco et al. 2014, Ripple et al. 2014, Bauer et al. 2015, Rust et al. 2016). To date, there appears limited evidence of integration of HCC research into management practice and policy formation (Miller 2015), potentially indicative of a research implementation gap. There are several possible reasons for this research-implementation gap. Given that HCC is a contentious and highly polarizing issue enmeshed within complex sociopolitical environments, implementing conflict mitigation strategies is often challenging (Treves and Karanth 2003). In many cases, conservation researchers may not effectively communicate their findings to managers, policy-makers, and decision-makers (Possingham 2009, Sunderland et al. 2009). Further, conservation efforts may be stymied by regional political climate given that centralized political and management agencies have had a reputation for mismanagement and corruption (Nelson 2010). Also, dynamics like these engender disputes between central agencies and local communities over management of natural resources (Gibson 1999, Nelson and Agrawal 2008). Given the breadth of challenges facing HCC, a single, all-encompassing means of achieving evidence-based conservation policy is unrealistic. However, there may be opportunities for improving conservation action by formulating scientific research in ways known to narrow the research-implementation gap.

Several widely-accepted frameworks to promote and guide research for actionability exist (i.e., promoting applicability and supporting decision-making via research) in management and policy arenas (Israel et al. 1998, Pullin and Knight 2001, Parker et al. 2005, Arts et al. 2006, Young 2007, Reid et al. 2016, Beier et al. 2017). Two broad principles are common to these approaches, notably, need for an explicit commitment to achieving conservation goals and need for collaboration at multiple levels and among multiple disciplines and stakeholders. Collaboration of this nature is deemed imperative for several reasons. First, cooperation of researchers, managers, and implementing agencies is necessary to increase the likelihood that research objectives and products will be relevant to conservation challenges (Balmford and

Cowling 2006, Haseltine 2006, Knight et al. 2008, Sunderland et al. 2009). Second, HCC issues have social, ecological, economic, and political dimensions that require collaboration across disciplines for researchers to arrive at a nuanced understanding of the problem and a realistic management solution (Campbell 2003, Mascia et al. 2003, Sunderland et al. 2009). Third, research-implementation often suffers when projects fail to include local stakeholders in the research process (Knight et al. 2008, Smith et al. 2009), as these groups offer valuable knowledge of local systems and improve relevance of research to their communities (Reed 2008, Kainer et al. 2009, Phillipson et al. 2012). Overall, actionable research frameworks provide guidance in understanding the complexity of HCC, improving connectivity between the research community and key decision-makers, and developing applicable solutions to mitigate HCC (Arts et al. 2006, Anyango-Van Zwieten et al. 2015).

Here I evaluate actionability of HCC research according to criteria associated with six actionability frameworks. My objective was to ascertain whether HCC research was designed and carried out in ways that are conducive to effective conservation implementation, particularly management action and policy formation. I use this review to address the need for increased dialogue and collaboration among academic institutions, management authorities, policy-makers, and local communities. While this analysis focuses on HCC research in East Africa, I also discuss applicability of results to a variety of scientific disciplines and geographic regions. To my knowledge, this is the first attempted analysis to elucidate actionability of published research revolving around human-carnivore conflict in this region and others.

5.3 Methods

5.3.1 *Literature Review*

I conducted a structured literature review to evaluate published papers of HCC research. I framed this review around HCC research occurring in East African countries of Kenya, Uganda, and Tanzania. Using Web of Science (URL: https://apps.webofknowledge.com/), I identified peer-reviewed papers addressing HCC in East Africa. This review was conducted using the following terms: TS= (human) AND (carnivore* OR felid OR canid OR lion OR leopard OR wild dog OR hyena) AND (conflict OR depredation OR predation OR attack*) AND (Tanzania OR Kenya OR Uganda OR East Africa). After this primary literature review, I systematically eliminated papers that fell outside the geographic scope of East Africa or were unrelated to HCC research.

Next, I evaluated papers for actionability according to a set of metrics derived from six frameworks: the Policy Action Approach (Arts et al. 2006), Research and Policy in Development (RAPID) (Young 2007), Co-producing Actionable Science (Beier et al. 2017), Community-Based Participatory Research (Israel et al. 1998, Parker et al. 2005), Evidence-Based Conservation (Pullin and Knight 2001), and the Continual Engagement Model (Reid et al. 2016). These metrics included 1) co-production of knowledge by co-authors from different institutions, 2) collaboration across disciplines, 3) intent to inform management and policy, and 4) stakeholder engagement. These metrics are described below.

5.3.2 *Analysis*

Co-production Co-production is a collaboration among researchers and decision-makers from a variety of institutions and agencies (Beier et al. 2017). In this way, co-production can represent a desire to engage policy- and decision-making bodies in the research process to make research more relevant (Young 2007, Reid et al. 2016). I conducted co-author analyses using affiliations to assess the level of inter-institutional collaboration among co-authors (Schummer 2004). With all co-author analyses I only selected the first listed affiliation, which in most instances can be assumed the primary affiliation of that author. Furthermore, the use of multiple affiliations for a single author in analyses can be considered pseudoreplication and could potentially bias results. For institutional affiliation, I placed the affiliated entity of each co-author into one of the following categories: academic institutions, government entities, private sector, or non-governmental organizations. While this measure of co-production is imperfect, it does provide insights into likelihood of the research proving actionable.

Collaboration Across Disciplines Broad collaboration across a diversity of disciplines is suggested as a method to improve actionability by authors of several frameworks (Israel et al. 1998, Reid et al. 2016, Beier et al. 2017). To date, a variety of different metrics measure multi-disciplinarity (e.g., co-occurrence of keywords in multiple disciplines, citations of papers from other disciplines). However, these methods can be inexact and often lead to unrealistic classifications of disciplines (Schummer 2004). An alternative method to assess disciplinary make-up of HCC research is using co-author affiliations as a measure of represented disciplines, assuming that each co-author makes a substantial contribution to the overall research (Schummer 2004). Although coarse, these methods have been effectively applied in similar efforts to assess interdisciplinary collaboration in conservation research (*sensu* Montgomery et al. 2018). I quantified co-authors using departmental affiliations and assigned them to one of 12 categories (Table 5.1). For non-academic entities (i.e., government agencies, NGOs, private industries), I placed co-authors into disciplinary categories based on mission statements of the organization wherever possible. I excluded any co-authors from disciplinary indices with affiliations that were too ambiguous to classify. I then calculated summary statistics and indices for both interdisciplinarity and multi-disciplinarity for the pool of papers extracted by this literature review. Interdisciplinarity is defined as collaboration with more than one discipline in one paper, whereas multi-disciplinarity relates to significance of a certain discipline among papers returned from this review. To assess interdisciplinarity, I used methods described by Schummer (2004) and examined number of co-authors occurring on a single paper who were from more than one discipline.

$$I^2\text{=number of papers having co-authors from} \geq 2 \text{ disciplines} / N$$

Here, N represents the total number of papers. Next, I determined each independent combination of disciplines and calculated an interdisciplinarity matrix ($c_{i,k}$) of bi-disciplinarity coefficients where

$$c_{i,k} = n_{i,k}/N \qquad (1)$$

$n_{i,k}$ is the number of papers co-authored by at least one author of both disciplines i and k. This matrix provides information on tendencies of disciplines to collaborate with one another. The discipline-specific interdisciplinarity indices (si_i) were also calculated, which represent relative involvement of each discipline in interdisciplinarity research.

$$si_i = \sum_{k \neq I} c_{i,k}/c_i \qquad (2)$$

For multi-disciplinarity, the number of disciplines involved in authorship was assessed to generate a multi-disciplinarity index (M). I selected a threshold of 5%, meaning that a discipline is represented by authorship in ≥ 5% of the total number of selected papers.

$$M^{.05} = \text{count}[c_i] \text{ if } c_i > 0.05 \qquad (3)$$

$$c_i = n_i/N \qquad (4)$$

Here, c_i represents the relative size of a given discipline (i) and n_i is the number of papers where one co-author is involved from i discipline. For comparative purposes, the relative size of the largest discipline was also calculated as:

$$c^{max} = \mathrm{Max}[c_i] \tag{5}$$

This measure is inexact but allows for better understanding of how researchers collaborate across disciplines and transcend their respective fields in pursuit of scientific inquiry. All indices resulted in proportions that were subsequently converted to percentages to allow for easier interpretation.

Intent to Inform Management and Policy Actionable science likely begins with a research team identifying a management or policy question requiring investigation (Beier et al. 2017). Such studies often provide information directly useful to managers and policy-makers (Pullin and Knight 2005, Young 2007). This intent can be equated to whether or not a research project is presented as applied or theoretical. To assess the degree to which research was applied or theoretical, I investigated mission statements of each journal where a paper was published. Based on these statements I placed papers into an 'applied', 'theoretical' or 'both' category, similar to methods used by Brook and McLachlan (2008). To be included in the 'both' category, the journal mission statement included interest in publishing both applied and theoretical research.

Stakeholder Engagement I determined if a paper incorporated local stakeholders in the research process (Israel et al. 1998, Reid et al. 2016, Beier et al. 2017). Since local stakeholders are seldom offered co-authorship, I searched methods sections for evidence of substantive engagement with local citizens and stakeholders. Their involvement was then ranked on a scale from 0 to 2. I awarded a '0' if no local stakeholders were mentioned in the methods section. Any surveying or interviewing of stakeholders by a primary author, including if a stakeholder was involved in translation, was given a score of 1. To earn a score of 2, stakeholders were directly involved in the research process (e.g., data collection, research design, development of research questions, etc.). While there are numerous other ways in which stakeholders can be involved, these three could be measured consistently across papers.

Evaluation I provided a summary evaluation of criteria for co-production, collaboration across disciplines, stakeholder engagement, and intention to formulate management and policy for each paper. As such, I used a binary scale for awarding points for meeting criteria in each category. For example, if a paper was authored by professionals from two or more disciplines, that paper would receive a 1 for collaboration across disciplines. The same process was followed for each of the other proxies in the same manner, with papers featuring the most beneficial characteristics (multiple organizations, the intent to inform policy formulation, and stakeholder engagement) earning a higher cumulative score. The paper with the highest cumulative score could be considered more actionable. I weighted metrics equally, as all are considered to influential on actionability of research, but admit that impact of an individual metric on actionability may vary depending on context. Difficulty justifying importance of one metric over another resulted in equal weighting. To assess the incorporation of actionable criteria temporally, I performed a linear regression with the hypothesis that recently published research would include more of these criteria. In addition, I calculated 95% confidence intervals and coefficient of determination (r^2) to display variability in scores and assess performance of the regression.

5.4 Results

My structured literature review yielded 80 papers. Of those, 34 were applicable for this study (i.e., exploring HCC in East Africa). Most papers were on research conducted in Kenya (n=20) and Tanzania (*n*=12), with far fewer in Uganda (*n*=2). These papers encompassed a wide variety of theoretical and applied research, ranging from animal behavior and physiology to testing reliability of boma construction. All papers used in this analysis were published after 1999, but the vast majority (*n*=28) were published after 2006 (Fig. 5.1). A total of 32.4% of papers focused on a combination of both small and/or large carnivores; 29.4% specifically addressed the human component of HCC while another 23.5% centered around lions. Additional HCC papers in East Africa were on spotted hyenas (5.9%; *Crocuta crocuta*) and African wild dogs (8.8%; *Lycaon pictus*). I excluded 9 co-authors from this analysis due to ambiguous affiliations. The mean number of co-authors in selected papers was 3.62 (SE=0.25) and ranged from 1 to 8.

In evaluating papers for co-production, most papers were co-authored exclusively by academics (64.7%; Fig. 5.2). Collaborations between academia and NGOs were also fairly common (26.4%; Fig. 5.2). Representation of co-authors from government entities was, however, minimal and mostly seen in collaborative efforts with academics or NGOs (5.8%), and I did not observe involvement of private industry in HCC research (Fig. 5.2). Only 32.4% of papers in this review featured collaborations among two or more institutional categories (Fig. 5.2).

Biology, ecology, and zoology (from here on biology) and wildlife management and conservation (from here on wildlife) disciplines were most well-represented in HCC research in East Africa, occurring in 73.5% and 35.2% of papers respectively (Fig. 5.3). Nearly two-thirds of the papers reviewed featured collaborations among two or more disciplines (I^2 = 61.8%) and several contained three or more (I^3 = 14.7%; Fig. 5.3). In assessing collaborations among disciplines, the two largest disciplines (biology and wildlife) were the most frequent collaborators, occurring in 23.5% of papers, followed by biology and the environmental sciences

(11.8%, Table 5.2). Furthermore, roughly 26.5% were solely authored by individuals from biology. Using a multi-disciplinarity index ($M^{.05}$), I found 6 disciplines represented in ≥ 5.0% of papers according to authorship. For disciplines that were less common in HCC research, interdisciplinary collaboration was high (89-100%; Table 5.2).

For intent to inform management and policy, papers from this analysis were published in 18 different journals. Most papers (61.7%) were applied while 23.5% were theoretical, and 14.7% were from journals that publish both applied and theoretical research. I also investigated local stakeholder engagement in research and found evidence of involvement in 58.8% of papers. Of those, 23.5% specifically interviewed or surveyed stakeholders, while 35.3% displayed evidence of incorporating stakeholders in the data collection process.

In evaluation of each papers compliance to criteria, scoring ranged from 0 to 4 with an average score of 2.1 (SE = 0.23). A total of 6 papers scored the maximum of 4 for meeting all criteria I assessed for being relevant to managers and policy-makers. Conversely, 6 papers received a score of 0 and did not meet any criteria. According to linear regression results, from 1999 to 2016 the trend appears to be slightly positive ($\beta = 0.08$; SE = 0.06), with recent papers meeting more criteria on average for generating relevant HCC research (Fig. 5.4). However, this pattern was relatively stochastic as evidenced by an r^2 of 0.12 for this linear regression (Fig. 5.4). Furthermore, effect sizes for this relationship were small and overall difference in average criteria met throughout the temporal range of this study was ~1 (Fig. 5.4).

5.5 Discussion

This analysis revealed that published HCC research in East Africa is primarily conducted by academics, with only 2 papers incorporating a co-author from a government agency. Roughly a quarter of papers in this review were published in theoretical journals (n=9), indicating that a desire to inform management and policy were not specific objectives. I also found that co-authors from disciplines outside of natural sciences were rarely included as collaborators in HCC research. Most notably, there were few papers with co-authors from social and political sciences. In contrast, local stakeholder engagement was common, as evidenced by over half of the papers (21 of 36) involving local stakeholders in research. However, degree of involvement of these stakeholders varied and could most often be described as minimal. The issue HCC in East Africa will continue to be a problem and topic of interest among researchers, managers, and policy-makers well into the foreseeable future. It is even more likely that problems of HCC will intensify as human populations expand and competition over limited space and resources increases (Treves and Karanth 2003, Graham et al. 2005). These forecasts further emphasize need for research that can inform interventionist action capable of diminishing HCC. Overall, the metrics I used to assess actionability of published papers could serve as a foundation for exploration of relevancy of conservation research in management and policy contexts across multiple geographic and temporal scales.

The research-implementation gap in HCC research was particularly evident when observing lack of co-authorship with individuals from organizations involved in governance. Although many papers were applied based on the journal in which they were published, few mentioned an explicit desire to inform management and policy. If a study was conducted to inform management and policy, an objectives section describing these goals would be appropriate and could allow for a clearer delineation of effective applications. Moreover, this trend may be driven by the current research-merit system, evidenced by the prevalence of academic co-authors in this analysis. This phenomenon is rooted in diminished value of management-applicable research in academia (Chapron and Arlettaz 2008, Arlettaz et al. 2010).

Methods aimed at improving relevance of research are also depicted as “slow science.” These types of characterizations can deter co-authors who are motivated by productivity and publication record. Publishing is a top priority for many scientists in North America and Europe, as a prestigious publishing record provides opportunities for projects and long-term funding. Conversely, metrics determining funding in developing countries tend to deviate from strictly publishing record, and may be influenced more by reputation, title, and professional network. Furthermore, mass media sources like television and newspapers may provide an alternative outlet for information, as they often reach a broader and diverse audience. However, as noted previously, these channels are not incentivized within Western academic institutions and are therefore less available for comprehensive review.

It has been suggested that interdisciplinary approaches tend to improve understanding of complex ecological and anthropogenic components of a problem (Balmford and Cowling 2006), subsequently enhancing research relevance. Although nearly 28% of identified papers focused on human aspects of HCC, individuals trained in social sciences were rarely included in papers, potentially indicating that co-authors are performing research outside their primary disciplines. I recognize that this proxy of co-author affiliations may not completely capture individual expertise and that competency in these disciplines can be obtained through unreported training and experience, but similar patterns showing a lack of interdisciplinary research were noted in a review of human-lion conflict (Montgomery et al. 2018). Reluctance to engage in interdisciplinary research may be primarily related to philosophical differences among disciplines and length of the research process (Campbell 2005). More specifically, social and conservation scientists indicated that differences in vocabulary, limited incentives for academics, lack of funding, and limited opportunities to collaborate are the biggest barriers to interdisciplinary research (Fox et al. 2006). In terms of conservation action, although interdisciplinary research can be challenging, rewards are broadly considered to outweigh costs, as these approaches can ultimately increase salience and success of conservation research (Mascia et al. 2003). Despite numerous calls for increased interdisciplinary research to improve conservation relevance and efficacy (Campbell 2003, Mascia et al. 2003, Thornhill 2003), I observed scant evidence of interdisciplinarity in HCC research in East Africa.

Most (77%) of the papers in this review were published in applied journals, and of those, many appeared to target management at local levels. This focus may reflect the appropriate scale of action in East Africa, where local management authorities may be more proactive in and better suited for implementing conservation initiatives. Moreover, despite publication of many HCC papers in applied journals, evidence of this research being actionable remains questionable. Again, this may stem from lack of decision-makers and boundary-spanning individuals included in the research process, as they serve as channels to improve research relevance and implementation. To effectively alleviate HCC in East Africa, increased collaboration between academic, government, and boundary-spanning organizations at multiple levels is critical.

Inclusion of local stakeholders was also fairly common within these papers, but acknowledge this often consisted of surveys or questionnaires where these individuals served as research subjects rather than participants in the research process. I recorded several instances where locals were trained in data collection and employed by researchers, a trend that was more common in recent papers. Although incorporation of stakeholders in data collection is important, ideally these groups would be engaged at the outset and would play a role in development of research projects. This involvement is often difficult to ascertain from published literature as including locals and, more often, communities as co-authors remains a seldom-used practice

(Castleden et al. 2010). Local knowledge is increasingly being recognized as a tool for effective conservation (Huntington 2000, Brook and McLachlan 2008) to enhance research and management efforts (Inglis 1993, Stevenson 1996). Inclusion of these groups in research also improves the likelihood of conservation implementation and success, because locals are more likely to adopt conservation recommendations stemming from research in which they actively participated (De Graaff et al. 2008). Further, engaging stakeholders early in the research process allows locals to develop research that meet their specific needs while subsequently empowering them to assume responsibility in management and conservation of their natural resources (Davidson-Hunt and O'Flaherty 2007).

The conservation sciences have aptly been termed a crisis discipline, where expedient action is necessary (Soulé 1985). The case of HCC in East Africa is no different, where human and carnivore livelihoods are hanging in the balance. Given these circumstances, it is important, as HCC researchers, to evaluate effectiveness and relevancy of this work in management and policy contexts. It seems that HCC research in this region is embracing some of the aforementioned challenges to bridging the research-implementation gap while largely ignoring others. The amount of community involvement identified in this analysis was positive and continued engagement and relationship building can only further improve relevance of research. Strides can still be made, however, in collaborating with disciplines outside of natural sciences, as well as with managers and policy-makers. However, I acknowledge that efforts to ameliorate this divide needs to occur collectively by both researchers and decision-makers, as conservation is often stymied without synergism between these groups. My analysis strictly focused on East Africa since high rates of HCC occur in this region, but this ultimately limited sample size. For this reason, I recognize that trends observed here are limited and may be specific to this particular region. I encourage further refinement of these methods and scalability across regions and conservation topics to elucidate broader trends. Although many factors play a role in the success of conservation action, the criteria outlined here can readily be utilized by researchers who are seeking to instill change and improve relevance of their research to management and policy formulation.

5.6 Acknowledgements

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APPENDIX

Table 5.1.

Discipline categories for co-authors conducting human-carnivore conflict research in East Africa**.**

Abbreviation	Description
W	Wildlife management and conservation
B	Biology, ecology, and zoology
F	Forestry
A	Agriculture
E	Environmental sciences
SS	Social sciences
PS	Political science, policy, and government
S	Statistics
GE	Geography
G	Geology
AN	Anthropology

Table 5.2.

Interdisciplinarity matrix and associated interdisciplinary indices for each discipline (si_i). Values represent percentage within papers (n=34).

$C_{i,k}$ (%)	W	B	F	A	E	SS	PS	S	GE	G	AN	si_i
W	8.8	23.5	0.0	0.0	5.9	0.0	0.0	2.9	2.9	0.0	0.0	75.0
B	23.5	26.5	0.0	5.9	14.7	0.0	0.0	2.9	2.9	2.9	0.0	64.0
F	0.0	0.0	0.0	2.9	2.9	0.0	0.0	0.0	0.0	0.0	0.0	100.0
A	0.0	5.9	2.9	0.0	2.9	0.0	0.0	0.0	0.0	0.0	0.0	100.0
E	5.9	14.7	2.9	2.9	2.9	2.9	0.0	0.0	2.9	0.0	2.9	88.9
SS	0.0	0.0	0.0	0.0	2.9	0.0	0.0	0.0	2.9	0.0	0.0	100.0
PS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0	100.0
S	2.9	2.9	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0	100.0
GE	2.9	2.9	0.0	0.0	2.9	2.9	2.9	2.9	0.0	0.0	0.0	100.0
G	0.0	2.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	100.0
AN	0.0	0.0	0.0	0.0	2.9	0.0	0.0	0.0	0.0	2.9	0.0	100.0

Figure 5.1.

Percentage of peer-reviewed publications (n=34) by year on human-carnivore conflict (HCC) in East Africa, 1999-2016.

Figure 5.2.

Percent representation of institution and inter-institutional collaboration of co-authors researching HCC in East Africa from 1999-2016. Uni = universities, academic institutions, and research centers; NGO = non-governmental, non-profit, and volunteer organizations; Gov = government funded institutions occurring at the national, regional, state, or local level; Prv = privately owned organizations or industry; I_I^2 = inter-institutional collaboration index that represents the percentage of papers that are co-authored by authors from ≥ 2 institutional categories.

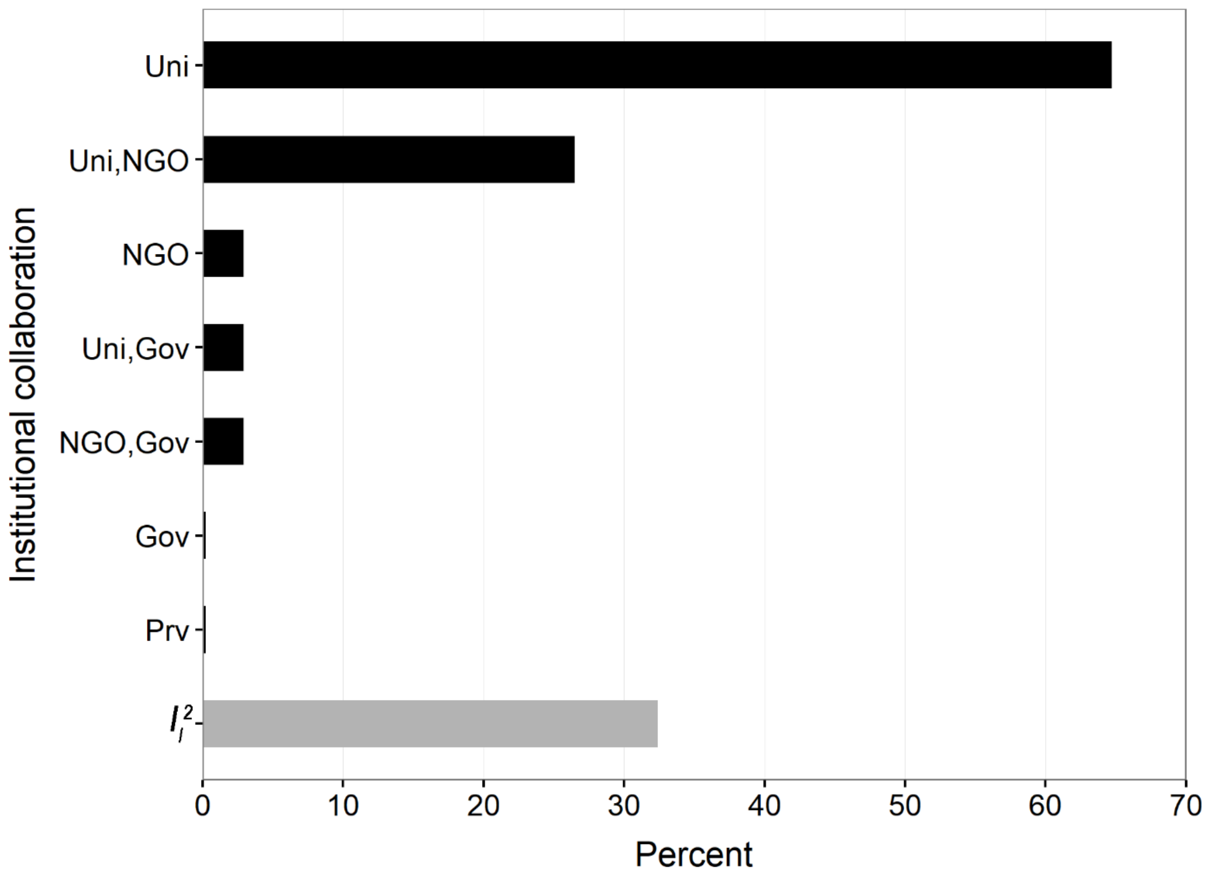


Figure 5.3.

Relative size of disciplines and measures of interdisciplinarity based on authorship of peer-reviewed publications on human-carnivore conflict (HCC) in East Africa from 1999-2016. Values are in percentages. B = biology, ecology, and zoology; W = wildlife management and conservation; E = environmental sciences; GE = Geography; AN = anthropology; A = Agriculture; SS = social sciences; S = statistics; PS = political science, policy, and government; G = geology; F = forestry; I^2 = interdisciplinary collaboration index that represents the relative percentage of papers that are co-authored by authors from ≥ 2 disciplinary categories; I^3 = interdisciplinary collaboration index that represents the relative percentage of papers that are co-authored by authors from ≥ 3 disciplinary categories.

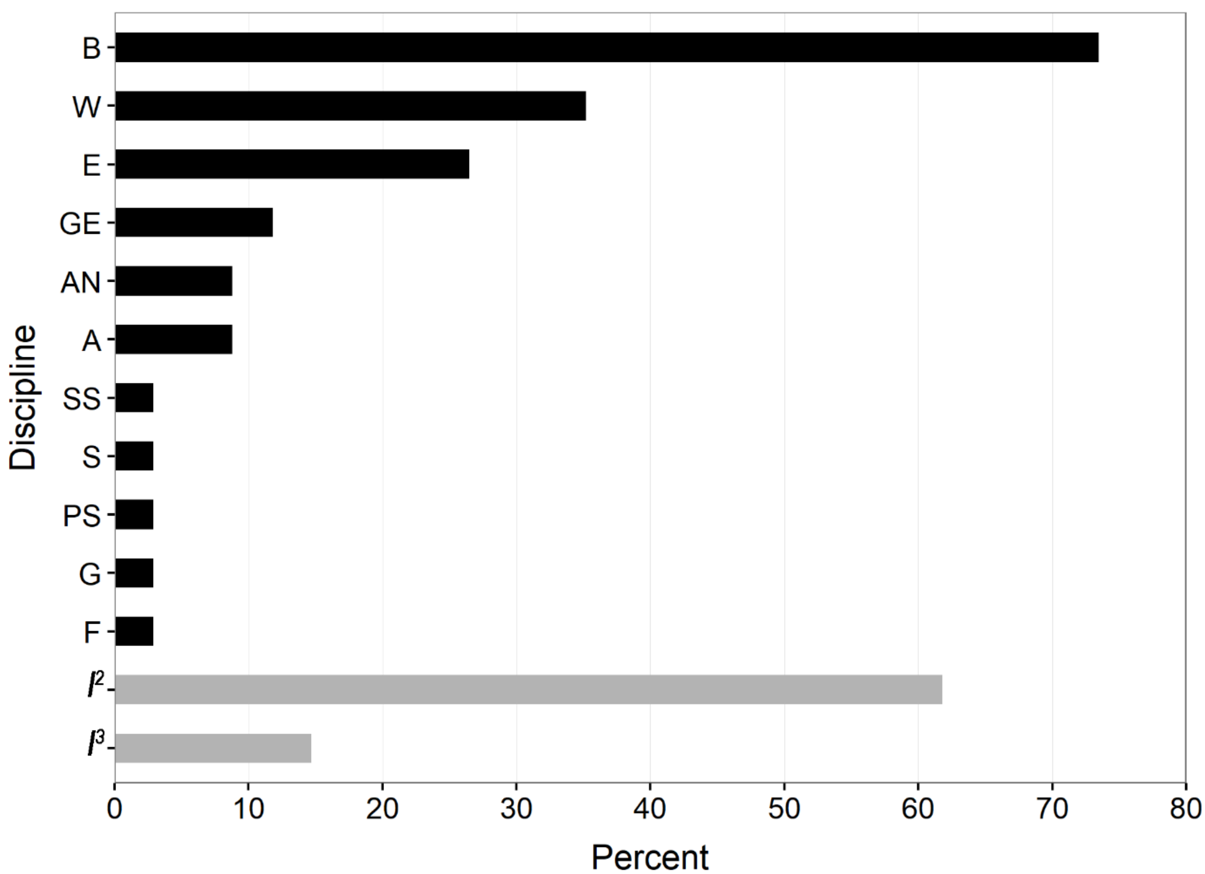
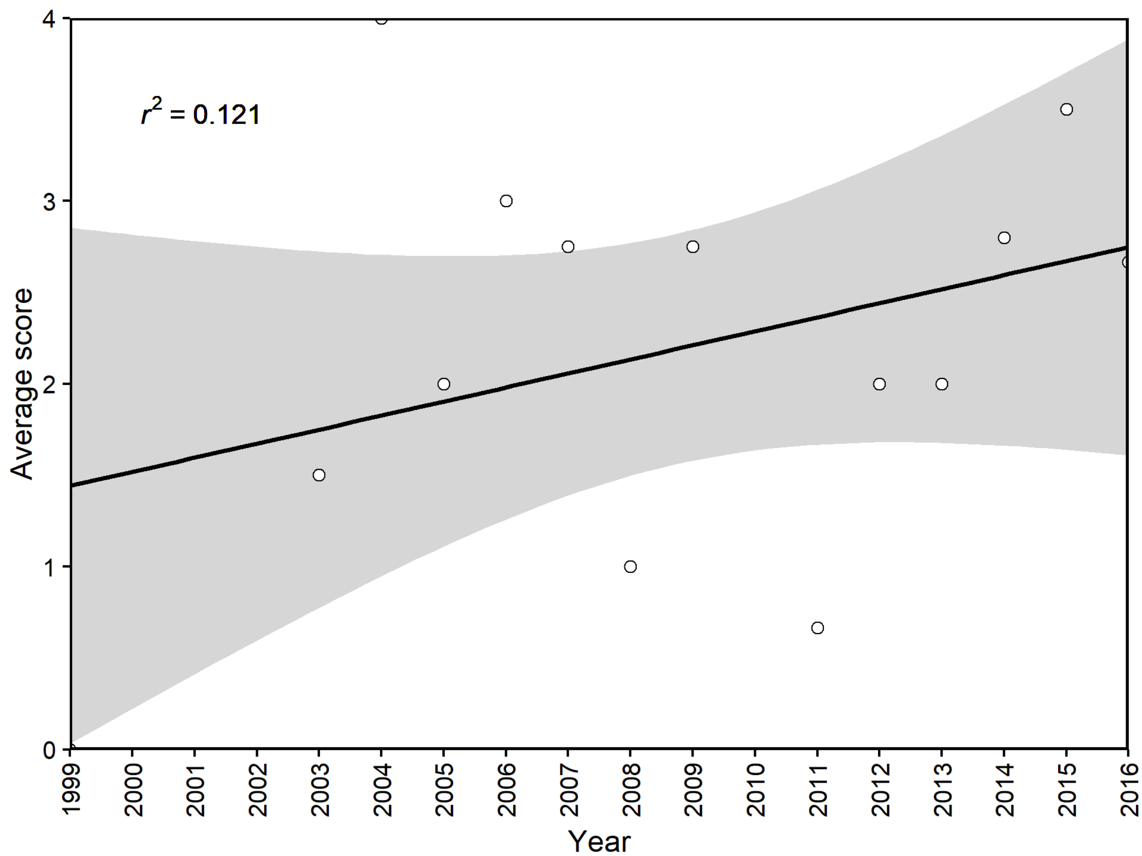


Figure 5.4.

Linear regression of the actionability of papers using the average score per year for papers published on human-carnivore conflict (HCC) in East Africa from 1999-2016.



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CONCLUSION

In this dissertation, I explored multiple topics and challenges at the forefront of wildlife science. Specifically, I investigated spatial ecology, human-wildlife conflict, and behavior of both native and non-native species. Each of these standalone research endeavors is rooted in a desire to inform species ecology and develop products applicable in conservation and management contexts. Broadly, this research has implications for conservation and management of native and non-native species, aiding in promoting the sustainability and health of human and natural systems.

Within each chapter of this dissertation, several broad lessons can be summarized. In Chapter 1, I provided an overview of current knowledge relating to wild pig behaviors and spatial ecology in North America. I highlighted current gaps in understanding that merit further research consideration, which include wild pig communication, movement ecology, effective control practices, and ecology at fine-scales and in newly colonized regions. In Chapter 2, I expanded on my literature review in Chapter 1 by exploring environmental impacts of a low-density wild pig population in Michigan. I found wild pigs to fit the role of an exotic engineer, as disturbance resulted in reduced vegetation cover, reduced diversity of plants of high conservation value, and increased leaching of macro-nutrients from soils. This work suggests that even at low densities wild pigs can influence biotic and abiotic components of a system, and indicates several aspects of the environment that may be impacted in recently colonized northern systems of the US. In Chapter 3, I explored fine-scale spatio-temporal correlates of movement states in wild pigs. I found proportion of some cover types, landscape structure, and weather to influence wild pig movement states. This research serves as the first attempt to use movement to assign behaviors in wild pigs, a method that is beneficial in promoting ecological understanding. My results may aid managers in developing control strategies to target individuals in a particular movement state using the spatio-temporal associations I observed. In Chapter 4, I investigated spatio-temporal dimensions of roaring in relation to a dominance shift in a group of reintroduced lions. Alterations in spatio-temporal signatures of lion roaring fills a knowledge gap in our understanding of the behavioral ecology of this species. Future investigations on spatio-temporal nature of roaring can be used to garner insights into habitat associations and to assess the viability and health of reintroduced lions. In Chapter 5, I examined the research-implementation gap in human-carnivore conflict (HCC) research being conducted in East Africa. This analysis revealed that actionability of HCC research could be improved with further interdisciplinary involvement, collaboration with decision-making entities, and integration of local stakeholders in the research process. While findings explicitly pertain to East Africa, it is possible that these trends hold for conservation research being conducted across a variety of taxa and geographic regions.

Overall, my research highlights the utility of fine-scale spatial data in investigations of species behavior and ecology. Research at fine spatio-temporal scales is becoming more prevalent with technological advances, presenting new and exciting avenues of ecological inquiry. In addition, my research on the behavior and ecology of non-native species can provide a foundation for future studies looking to explore the function and impact of these species in newly colonized systems. By investing in research at the beginning of a potential invasion, managers can use research findings to develop strategic and informed control strategies that may be more effective in promoting eradication. Lastly, increased collaboration among researchers, practitioners, disciplines, and stakeholders will aid in production of salient and actionable research capable of meeting conservation and management goals.