Determining habitat requirements and landscape factors for the decline of the southeastern pocket gopher (*Geomys pinetis*)

by

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Abstract

Southeastern pocket gophers (*Geomys pinetis*) are rodents of conservation concern endemic to open-canopy pine forests in the southeastern United States. Preserving habitat is critical for long-term conservation, but there is uncertainty about patch- and landscape-level variables influencing species presence. I hypothesized *G. pinetis* presence would be influenced by patch-level characteristics (e.g. canopy cover, ground cover). I tested this hypothesis using vegetation and presence surveys across the species' range. Results indicated that *G. pinetis* presence is influenced by vegetation characteristics at multiple scales. However, many historically occupied areas with suitable vegetation no longer support populations. I hypothesized landscape factors such as fragmentation and urbanization negatively influence *G. pinetis* persistence. To test this hypothesis, I examined historically occupied sites with recent re-surveys to assess persistence. My results indicated that persistence was influenced by human development and other landscape characteristics. Conservation efforts should aim for areas with intermediate canopy and an herbaceous understory embedded in undeveloped landscapes. These results can information management-decision tools to prioritize areas for habitat manipulations, translocations, and restoration.

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List of Abbreviations

gSSURGO	gridded Soil Survey Geographic Database
AICc	Akaike's Information Criterion for small sample sizes
CC	Canopy closure
NLCD	National Land Cover Database

Chapter 1: Determining habitat requirements at multiple scales for the southeastern pocket gopher (*Geomys pinetis*)

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Abstract

The southeastern pocket gopher (*Geomys pinetis*) is a fossorial rodent endemic to pine forests in the southeastern United States. Southeastern pocket gophers are ecosystem engineers that provide vital services such as soil aeration and nutrient cycling; however, they are declining across their range. Conserving the species' habitat is critical for long-term conservation and management, but there is uncertainty about specific variables influencing species presence. My objective was to determine vegetation characteristics associated with southeastern pocket gopher distribution at both the home-range scale (0.09 ha) and the local scale (100 ha). To address that objective, I assessed pocket gopher presence and conducted vegetation surveys at 177 sites during the growing seasons (March-September) of 2016-2017. At the local scale, I found the top model included variables related to understory structure and canopy closure. I found the top model for home-range scale included variables for food resources and canopy closure. Conservation efforts should aim for areas with intermediate canopy closure (between 45-55% closure), little vertical structure, and an understory dominated by grasses and forbs – presumably for food resources. The restoration of southeastern pocket gopher habitat should explicitly consider multiple spatial scales since occupancy was affected by different vegetation variables at the two spatial scales.

Introduction

The southeastern pocket gopher (*Geomys pinetis*) is a fossorial rodent historically associated with the longleaf pine (*Pinus palustris*) ecosystem that once dominated the Coastal Plain of Alabama, Georgia, and Florida (Engstrom 1993, Hickman and Brown 1973, Pembleton and Williams 1978, Simkin and Michener 2005, Van Lear et al. 2005). Since European settlement, the longleaf pine ecosystem has experienced dramatic losses and is now estimated to occupy <3% of the original range (Landers et al. 1995, Van Lear et al. 2005). With the dramatic loss of longleaf pine forests, *G. pinetis* have also declined and are now a species of conservation concern throughout their range (Alabama Department of Conservation and Natural Resources 2015, Florida Fish and Wildlife Conservation Commission 2012, Ozier 2010). In recent years, restoration of the longleaf pine ecosystem has been a high priority in many state wildlife action plans, and those restoration efforts include the need to restore valuable faunal species like *G. pinetis* (Alabama Department of Conservation and Natural Resources 2015, Florida Fish and Wildlife Conservation Commission 2012, Georgia Department of Natural Resources 2015).

G. pinetis is of conservation importance because, as an ecosystem engineer, it improves ecosystems functionality, enhances resilience, and promotes diversity (Jones et al. 1994, Reichman and Seabloom 2002). *G. pinetis* tunneling and burrowing activities affect ecosystem services such as soil aeration, water infiltration, and litter decomposition which can impact seedling recruitment and vegetation heterogeneity (Forbis et al. 2002, Kalisz and Stone 1984). The tunnels created by *G. pinetis* also provide refugia for several species of commensals, including 14 unique species of invertebrates (Cartwright 1939, Ozier 2010, Skelley and Gordon 2001). Additionally, a number of federally listed species like the gopher frog (*Lithobates capito*) and the eastern indigo snake (*Drymarchon couperi*) use *G. pinetis* tunnel systems for shelter and foraging (Blihovde 2006, Miller et al. 2012). Because of the benefits *G. pinetis* provide to the longleaf pine ecosystem, conserving and restoring their populations are warranted.

Like many species of conservation concern, conserving *G. pinetis* habitat is critical for long-term restoration and management. Recent studies of *G. pinetis* habitat offer valuable information but leave uncertainty with regard to actionable management objectives. Warren et al. (2017a) assessed habitat in a well-managed longleaf pine forest in southwestern Georgia and found significant differences in 'used' versus 'unused' sites regarding soil composition with *G. pinetis* preferring areas with sandier soil compositions. However, they found no differences in understory vegetation characteristics. Similarly, in southeastern Alabama soil characteristics for sites used by *G. pinetis* had <8.05% clay in the upper 20 cm of soil (Bennett 2018). In addition, occupancy was associated with intermediate levels of canopy cover (Bennett 2018). Although these two studies had important conservation implications, soil texture is not a factor that can be readily controlled by management (Wakatsuki and Rasyidin 1992). However, these studies each evaluated habitat selection across a limited area that may not have included all vegetation types *G. pinetis* can inhabit.

Additional research across a range of forest types and at multiple scales may elucidate relationships between *G. pinetis* occupancy and vegetation structure and composition which can be manipulated using common management techniques. Studies have highlighted the importance of evaluating patterns at a variety of biologically significant spatial scales for not only management objectives but also for understanding underlying ecological mechanisms (Levin 1992, Mayor et al. 2009, McGarigal et al. 2016, van Beest 2010, Razgour et al. 2011). Habitat selection studies benefit from this integrative approach because it often permits identification of limiting factors at a specific scale which are affecting processes at other scales (Mayor et al. 2009). Commonly, habitat selection is thought of in terms of hierarchical levels. In particular, habitat selection can occur at four levels based on the idea that animals select different resources at different scales and the availability of those resources depends on the other hierarchical levels (Johnson 1980). Previous work on *G. pinetis* studied second-order level selection, which focuses on characteristics that an individual would select to determine its home range (Warren et al. 2017a, Bennett 2018). This level is then conditional upon the first-order level, which is the selection of a geographic range (Johnson 1980). However, additional scales have not been studied for *G. pinetis*.

Due to the lack of knowledge surrounding additional scales of resource selection, the goal of my research was to assess selection at two scales using data from the entire species' range. The two levels were the second-order selection, (i.e. the home-range scale) and an intermediate level between the second and first-order selections (i.e. the local scale) based on presence of *G pinetis* within a 1 km^2 plot. I hypothesized that increases in canopy density and structural complexity of understory would decrease the likelihood of *G. pinetis* occupancy; whereas, increases in food resources and availability of suitable soils would increase the likelihood of *G. pinetis* occupancy (Table 1.1). At the local scale, I predicted *G. pinetis* would select areas of low structural complexity such that occupancy would be positively related to lower basal area and canopy cover. This prediction is based on *G. pinetis* associations with areas of little understory and woody structure such as open pine savannas, grasslands, pastures, and roadsides (Avise and Laerm 1982, FWC 2012, Southern Wildlife Consults 2008). At the home-range scale, I predicted *G. pinetis* would select areas where food resources, such as forbs and grasses, were abundant and understory structure was low. My predictions are based on *G. pinetis* avoidance of areas with dense root systems (Ford 1980) and other gopher species' tendency to choose areas with greater forage (Connior et al. 2010, Cox 1989). Finally, I predicted that there would be preferred vegetation characteristics that could be enhanced or restored through land management despite the strength of soil characteristics as a predictor of *G. pinetis* presence.

Methods

Study Site Selection

I selected study sites within the historic range of the species in Alabama, Georgia, and Florida (32,844,400 ha) (IUCN 2008) (Figure 1.1). I generated a 1-km^2 grid across *G. pinetis* range in ArcMap (Homer et al. 2012, ESRI 2015). I selected grid cells for random selection that contained ≥50 percent of land cover classes historically associated with *G. pinetis*, which included evergreen forests, mixed forests, shrub/scrub, grasslands/herbaceous, pasture/hay, and cultivated crops (Avise and Laerm 1982, Homer et al. 2012). In Georgia and Florida, I used the Create Random Points tool in ArcMap to place points in grid cells, and if those grid cells could be accessed, they were added as a study site (Georgia Department of Natural Resources 2015, Florida Natural Areas Inventory 2016). In Alabama, I stratified the selection of sites on public and private land by first creating the 1-km^2 grid only within public lands in Alabama (Conservation Biology Institute 2012). I then randomly selected 75 grid cells on public lands, and they became study sites if they were accessible. For private sites, I repeated the process above, but with private lands. Because of the difficulty all states had in finding single ownership private lands that were large enough to fully contain a study site, I chose sites more opportunistically by finding private lands as close as possible to the original randomly selected grid square. I then created a smaller 500 m^2 square inside of the original 1 km^2 square (Figure

1.2) which would act as the survey path to avoid double sampling in the case two squares were adjacent to each other.

Transect Surveys

I conducted *G. pinetis* presence surveys and measured habitat attributes during the growing seasons (approximately April through September) of 2016 and 2017. For each survey, two observers walked along the 500 m^2 inside-square (2000 m total length), scanning the ground for *G. pinetis* mounds, which I used as an indicator of presence (Harper 1912, Warren et al. 2017a, b). Because one animal can create several mounds, I recorded the location at the center of the cluster of mounds (Ford 1980). I defined a cluster as ≥ 3 mounds that were ≤ 5 meters apart since *G. pinetis* are territorial and unlikely to have overlapping tunnel systems (Ford 1980). Additionally, I recorded the number of mounds, number of fresh mounds, distance along the survey line, and distance from the survey line for each mound cluster.

I recorded vegetation characteristics at each mound cluster encountered but not exceeding 10 clusters. I also measured vegetation at subplots placed every 200 m along the transect regardless of *G. pinetis* presence. Canopy closure was measured in each cardinal direction around the center of the cluster or subplot using a spherical convex densiometer (Baudry et al. 2014). I used a 1 m^2 frame to record percentage of ground cover that was bare ground, leaf litter, woody vegetation, forbs, and grasses (Daubenmire 1959, USDA 1999). I recorded vertical cover at each cardinal direction, four meters from the center of the mound cluster or subplot, using a 1.22 m tall Robel pole (Smith 2008, Toledo et al. 2002). Basal areas of pines and hardwoods were recorded with a 10 Basal Area Factor (BAF) cruising prism (JIM-GEM Rectangular Prism, Clear, Forestry Suppliers, Jackson, MS) (USDA 1999).

Soil Survey Data

I downloaded gridded Soil Survey Geographic Database (gSSURGO) information for Alabama, Georgia, and Florida (Soil Survey Staff). I overlaid each 1-km^2 survey site with the soil polygons, and then calculated the area occupied by each soil texture class within each site. Because the high number of texture classes (n=26), I reclassified texture classes as highly suitable, suitable, or unsuitable (Table 1.2) (Bennett 2018, Warren et al. 2017a). Due to the low spatial resolution of the gSSURGO data (30 m), I only calculated percentage of soil classes for the local scale (Soil Survey Staff).

Data Analysis

Before creating candidate models, I evaluated variables for correlation using the *car* package in program R (Fox and Weisberg 2011, R Core Team 2019). Canopy closure and total basal area were correlated so I proceeded with canopy closure, which I believe is more biologically important. For each spatial scale, I evaluated a set of models representing *a priori* hypotheses about whether occupancy was driven by food resources, understory structure, or canopy (Table 1.1).

For the local scale, I averaged the measured variables from the systematic plots of each site. I then modeled site-level occupancy with logistic regression. I compared the models using adjusted Akaike's Information Criterion for small sample sizes (AICc) where the most parsimonious model has the lowest AICc value (Akaike 1998, Anderson and Burnham 2002). I evaluated model fit using the concordance statistic (c-statistic) (Austin and Steyerberg 2014).

Following Johnson (1980), I limited analyses to occupied sites for the home-range scale. I used logistic regression with a random site effect to examine factors discriminating occupied clusters from unoccupied systematic plots. Focusing on the same hypotheses as site-level analysis, I compared the top models using AICc (Anderson and Burnham 2002). I considered competing models to be ones that fell within 2 AICc units of each other. I performed all analyses in R (R Core Team 2018).

Results

Local Scale

I surveyed 177 sites across Alabama (n=56), Georgia (n=70), and Florida (n=51). Site-level detection was highest in Florida and lowest in Alabama. I detected *G. pinetis* at 38 (21.5 %) sites, with Alabama having two (3.6%) sites occupied, Georgia having 17 (24.3%) sites occupied, and Florida having 19 (37.3%) sites occupied.

The top two models to explain *G. pinetis* occupancy included effects of structure and tree canopy variables (Table 1.3). Both models indicated a negative relationship with *G. pinetis* occupancy and increasing groundcover vegetation height and no effect of shrub groundcover. The best model (i.e., lowest AICc) included the average vertical height of groundcover, percentage of woody vegetation as ground cover, and a quadratic effect of canopy closure (Table 1.3, Fig. 1.3). For every 1% increase in groundcover of shrubs, a site was 1.00 (0.96, 1.05, 95% C.L.) times as likely to be occupied by *G. pinetis*. For every 2.5 cm increase in groundcover height, a site was 1.2 (1.1, 1.3, 95% C.L.) times less likely to be occupied. Occupied sites occurred over a range of canopy closure, but the greatest probability of occupancy was ~48% canopy closure (Figure 1.3). A closely competing model included the average height of ground cover and percentage of woody vegetation as groundcover although there was no effect of woody vegetation as groundcover (Table 1.3). For every 1% increase in shrubby groundcover, a site was 1.00 (0.96, 1.04, 90% C.L.) times as likely to be unoccupied by *G. pinetis*. Additionally, for every 1 in. increase in groundcover height, a site was 1.2 (1.1, 1.3, 95% C.L) times as likely to be unoccupied. The concordance statistic indicated good predictive ability of both the top models (C=0.767 and 0.760, respectively) (Austin and Steyerberg 2012).

Home-range Scale

Within the 38 occupied sites, we surveyed 675 plots. These plots contained both *G. pinetis* clusters and systematic plots along survey transects (occupied plots n=296, unoccupied plots n=379). At occupied sites we measured an average of 8 mound clusters (median=10.0, SD=3.1); 24 sites had more than 10 clusters observed (max: 96), with only the first 10 clusters being measured.

The top model for home-range scale included groundcover of grasses and forbs and a quadratic effect of canopy cover (AICc weight=0.68) (Table 1.5, Fig. 1.4). For every 1% increase in groundcover of grasses, a plot was 1.01 (1.007, 1.019, 95% C.L.) times as likely to be occupied by *G. pinetis*. Based on this model, there was no conclusive relationship with forbs because for every 1% increase in forbs as groundcover, a plot was 1.00 (0.99, 1.01, 95% C.L.) times as likely to be unoccupied by *G. pinetis.* Similar to what was seen as the local-landscape scale, the highest probability of occupancy was at an intermediate level of canopy closure (~48%) (Figure 1.4).

Discussion

For the local scale, the hypothesis that increasing structural complexity of the understory would decrease the probability of *G. pinetis* occupancy was supported by the top two models. The structure model, which included the average height of groundcover and the percentage of shrubs and woody groundcover, was present in the top four model rankings (Table 1.3). Past studies of *G. pinetis* have found that the species is associated with areas of sparse woody understructure, such as that seen in frequently burned longleaf pine forests (Avise and Laerm

1982, Southern Wildlife Consults 2008). Areas with great woody groundcover may be avoided because it is energetically more expensive for *G. pinetis* to create tunnel systems through dense root systems since the roots needs to be excavated around or bitten through (Hickman and Brown 1973, Vleck 1979, Ford 1980, Vleck 1981). Similar patterns have been observed in other gopher species, with many selecting areas of low woody structure such as meadows, tallgrass prairies, and grasslands (Benedix 1993, Huntely and Inouye 1988, Jones et al. 2008).

Although soil characteristics have been the best predictors of *G. pinetis* occupancy in previous studies, (Bennett 2018, Warren et al. 2017a), the hypothesis that greater availability of suitable soil would increase occupancy was not supported. Others have used SSURGO data to identify patterns in pocket gopher distribution. However, those studies found stronger relationships between past land use practices and amount of available forage than to the soil characteristics (Connior et al. 2010, Hoffman et al. 2007). Wagner et al. (2014) noted that edaphic variables collected from SSURGO were predictors of Louisiana pine snake (*Pituophis ruthveni*) habitat at two spatial scales. However, the smallest spatial scale evaluated was 100-ha (the minimum multi-year home range for the species) which is the largest spatial scale we assessed. The SSURGO data, available at a spatial resolution of 30 m (Soil Survey Staff) is likely too coarse to observe relationships with *G. pinetis* occupancy.

My hypothesis that *G. pinetis* occupancy would decrease with increasing canopy closure was only partly supported at the local-landscape level. The top model included a quadratic function of canopy closure where survey sites with intermediate canopy closure had the highest probability of occupancy (Figure 1.3). The trend with canopy closure was also observed by Bennett (2018) in central Alabama, with the highest probability of *G. pinetis* occupancy at sites with around 49% canopy cover. Shading provided by intermediate canopy may slow the loss of soil moisture which is necessary to maintain tunnel structure while also stimulating plant growth into tunnels (Hickman and Brown 1973). Additionally, shade associated with dense canopy decreases abundance of understory vegetation such as grasses and forbs, which are common food resources for *G. pinetis* (Gates and Tanner 1988, Hickman and Brown 1973). Survey sites with dense canopy closure were often hardwoods that would be unlikely to support *G. pinetis*. *G. pinetis* have been found in areas with little to no canopy closure such as fields, along roadways, and in agricultural fields (FWC 2012, Southern Wildlife Consults 2008). However, many of my low canopy sites were frequently tilled fields, hard-packed roads, or recently clear cut areas which are likely unsuitable for the species.

Canopy closure was an important predictor at the home-range scale, but food resource variables were also important at this scale. The hypothesis that increasing amounts of food resources would increase the probability of occupancy at the home-range scale was supported. While there is little research regarding on diet of *G. pinetis*, grasses and forbs have been found within their caches (Ross 1976). Warren et al. (2017a) and Bennett (2018) also found greater percentages of grasses at occupied sites. It is unusual that the top model predicts no relationship between increasing amounts of forbs and *G. pinetis* occupancy. For other gopher species, forbs are the preferred food resource even when abundance of grasses is great (Connior et al. 2010, Rezsutek and Cameron 2011).

Probability of *G. pinetis* occupancy was related to different habitat variables at the two different scales. We found that at the local scale, the complexity of understory and the canopy closure affected *G. pinetis* occupancy. However, at the finer home-range scale, the abundance of food resources along with canopy were better indicators of occupancy. Determining the limiting factors at the two different scales is an important step in understanding limits on *G. pinetis* distribution and identifying areas for conservation planning.

Several important management implications arise from our research. Restoring *G. pinetis* habitat should explicitly consider multiple spatial scales. Within areas with suitable soils, managing for a forest with intermediate canopy closure, little understory structure, and an understory dominated by grasses and forbs should benefit *G. pinetis*. In longleaf pine forests, maintaining frequent fire intervals facilitate all of these objectives by limiting the amount hardwood species in the midstory and understory and promoting understory diversity of native grasses and forbs (Brockway and Lewis 1997, Gates and Tanner 1988).

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Tables and Figures

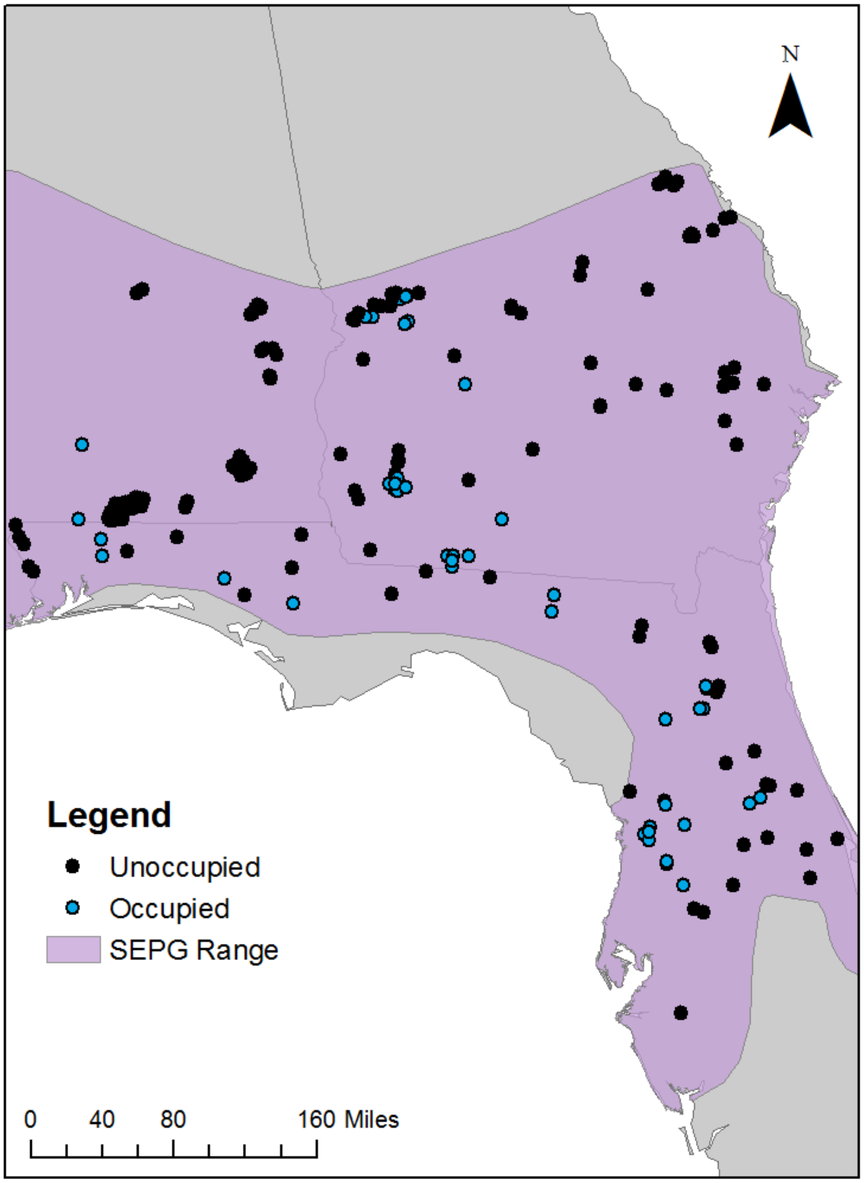

Figure 1.1: Mapped locations of surveys from 2016-2017 within *G. pinetis* historic range (purple). The black points indicate sites that were unoccupied at the time of survey; whereas, blue points were sites with *G. pinetis* mounds present at the time of survey.

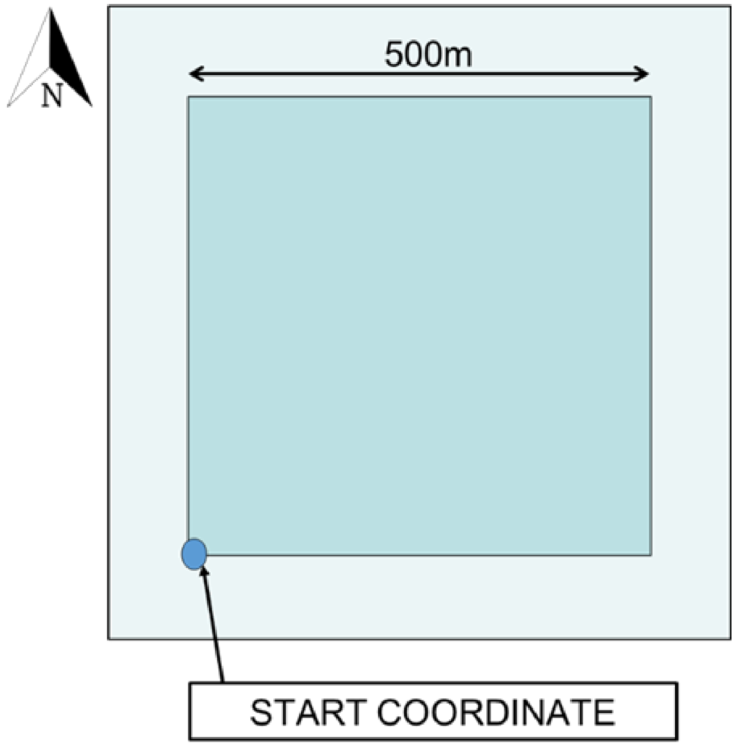

Figure 1.2: Each 1 km^2 site was surveyed for *G. pinetis* by two observers walking from the start coordinate, along the inner 500 m^2 square, north (for one individual) and east (for the other individual) which ensured two independent surveys.

Table 1.1. Predictions regarding relationships between habitat variables and *G. pinetis* occupancy among candidate models

Model	Variables	Prediction
Canopy	Canopy Closure (%)	With increasing canopy closure, *G. pinetis* occupancy will decline
Food Resources	Groundcover of Grasses (%) and Forbs (%)	With increasing percentages of grasses and forbs, *G. pinetis* occupancy will increase
Soil	Area of Suitable Soil (%)	With increasing percentages of suitable soils, *G. pinetis* occupancy will increase
Structure	Understory Height (in.) and amount of Shrubs as groundcover (%)	With increases in vegetation height and percentages of woody groundcover, *G. pinetis* occupancy will decrease

Table 1.2. Soil suitability categories based on gSSURGO texture classes for *G. pinetis* occupancy

Reclassification	**Original Texture Class**
Highly Suitable	Fine sand Fine sandy loam Loam Loamy coarse sand Loamy fine sand Loamy sand Sand Sandy loam Silt loam
Suitable	Coarse sand Coarse sandy loam Gravelly coarse sand Gravelly fine sandy loam Very fine sandy loam
Unsuitable	No data available Bedrock Clay Clay loam Muck Mucky fine sand Mucky peat Paragravelly sandy clay loam Sandy clay Sandy clay loam Silty clay Silty clay loam

Table 1.3. Local scale model suite selection for variables influencing *G. pinetis* occupancy across Alabama, Florida, and Georgia.

Model	Parameters	AICc	ΔAICc	w_i
Structure + Canopy (CC^2)	5	165.8	0	0.6
Structure	3	167.6	1.8	0.2
Structure + Food	5	169.6	3.9	0.1
Structure + Soil	4	169.7	3.9	0.1
Canopy (CC^2)	3	178.3	12.5	$1.0e^{-3}$
Soil + Canopy (CC^2)	4	179.2	13.2	$7.2e^{-4}$
Food + Canopy (CC^2)	5	181.3	15.5	$2.6e^{-4}$
Intercept Only	1	186.1	20.4	$2.3e^{-5}$
Soil	2	186.2	20.5	$2.1e^{-5}$
Food	3	187.1	21.3	$1.4e^{-5}$
Food + Soil	4	188.1	22.3	$8.5e^{-6}$

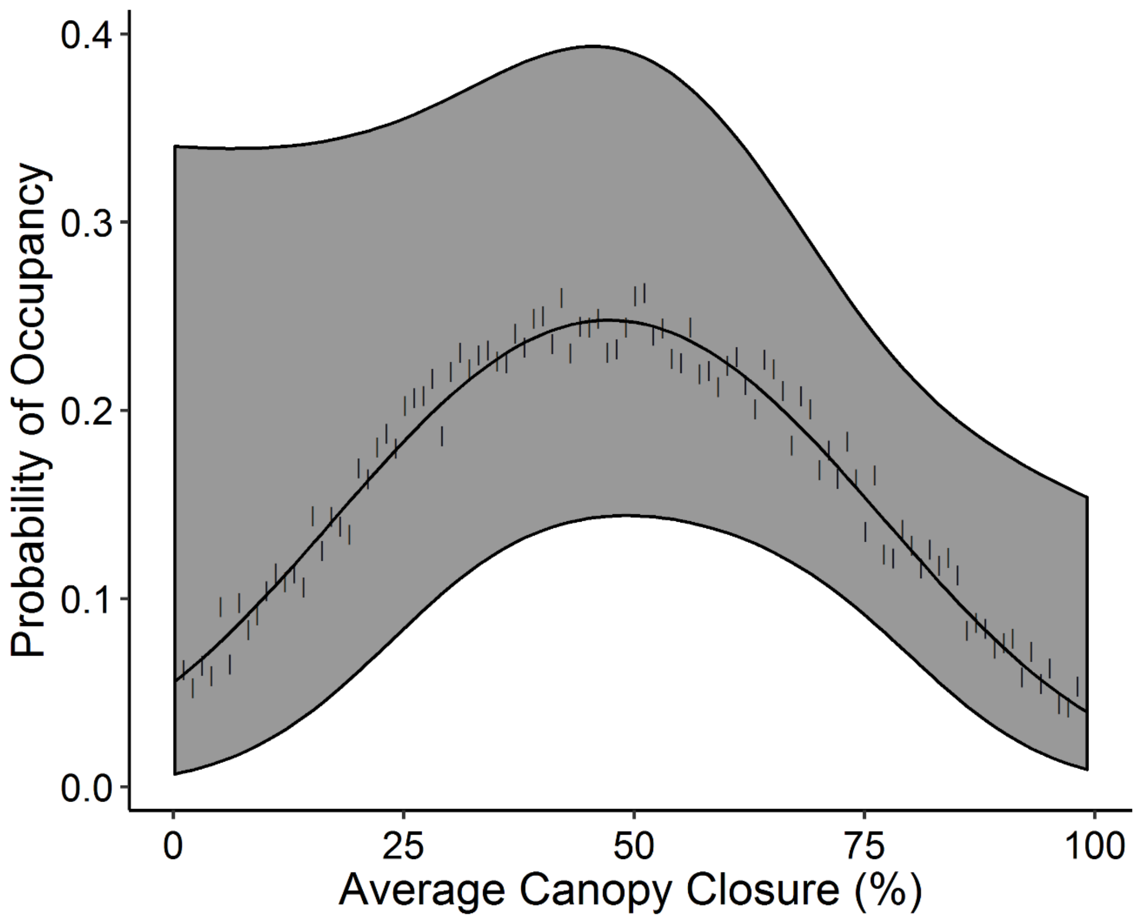

Figure 1.3. Influence of average canopy closure (%) on the probability of *G. pinetis* occupancy at the local scale (the bands represent the 95% confidence envelopes)

Table 1.4. Mean (95% confidence limits) for local scale vegetation variables across all 177 sites sampled for presence of *G. pinetis* in Alabama, Georgia, and Florida. Occupied sites had *G. pinetis* mound clusters present; unoccupied sites had no *G. pinetis* mound clusters detected during surveys.

Variable	Occupied (n = 38 sites)	Unoccupied (n = 139 sites)
Canopy Closure (%)	58.6 (52.2, 65.1)	67.0 (63.0, 70.9)
Vertical Height (in.)	4.3 (3.0, 5.7)	9.7 (8.4, 10.9)
Bare/Sand (%)	19.8 (14.7, 24.8)	11.7 (9.8, 13.6)
Litter (%)	32.1 (25.7, 38.4)	40.4 (37.3, 43.6)
Grasses (%)	20.1 (15.6, 24.6)	16.7 (14.8, 18.6)
Forbs (%)	8.2 (6.0, 10.5)	9.4 (8.2, 10.6)
Shrubs/Woody (%)	13.0 (8.7, 17.4)	17.7 (15.9, 19.4)
Pine BA (ft^2/acre)	29.8 (24.0, 35.7)	36.7 (32.9, 40.6)
Hardwood BA (ft^2/acre)	14.6 (10.6, 18.6)	25.8 (21.7, 29.8)

Table 1.5. Home-range level model suite selection for variables influencing *G. pinetis* occupancy.

Model	Parameters	AICc	ΔAICc	w_i
Food + Canopy (CC^2)	6	898.7	0.0	0.7
Structure + Food	6	901.1	2.3	0.2
Structure + Canopy (CC^2)	6	902.7	4.0	0.1
Food	4	908.6	9.9	$5.0e^{-3}$
Canopy (CC^2)	4	914.1	15.4	$3.1e^{-4}$
Structure	4	919.1	20.3	$2.6e^{-5}$
Intercept Only	2	929.5	30.8	$1.4e^{-7}$

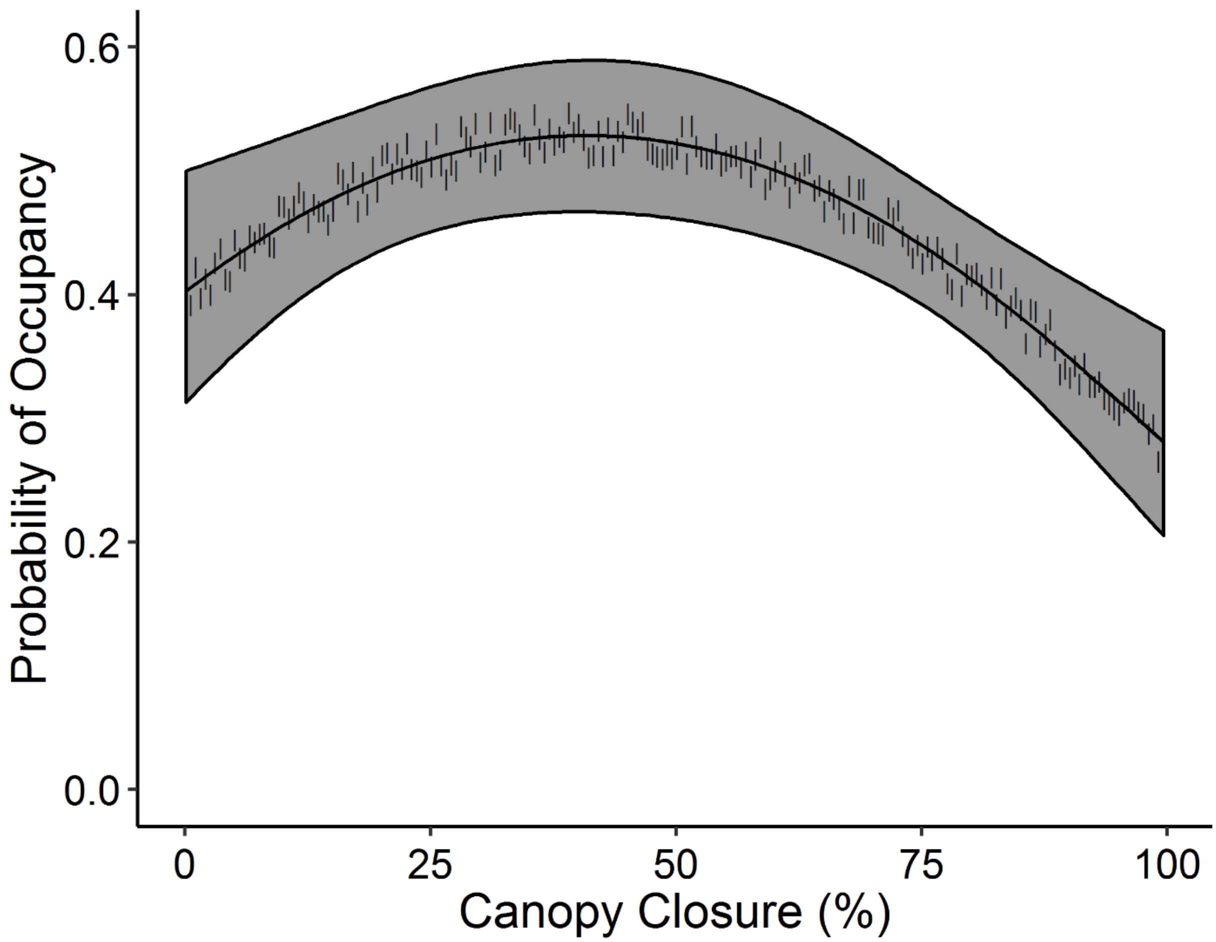

Figure 1.4. Influence of average canopy closure (%) on the probability of *G. pinetis* occupancy at the home-range scale (the bands represent the 95% confidence envelopes)

Table 1.6. Mean (95% confidence limits) for home-range scale vegetation variables across all 38 occupied sites sampled for presence of *G. pinetis* in Alabama, Georgia, and Florida during 2016 and 2017. Plots with mound clusters were occupied by *G. pinetis*; unoccupied plots without clusters were systematic plots along survey transects.

Variable	**Occupied (n = 296 plots)**	**Unoccupied (n = 379 plots)**
Canopy Closure (%)	51.6 (48.1, 55.1)	58.7 (55.4, 62.0)
Vertical Height (in.)	3.0 (2.5, 3.4)	4.3 (3.7, 5.0)
Bare/Sand (%)	20.5 (17.6, 23.4)	19.6 (16.8, 22.4)
Litter (%)	23.0 (19.5, 26.4)	32.0 (28.5, 35.5)
Grasses (%)	31.0 (27.5, 34.5)	20.1 (17.5, 22.7)
Forbs (%)	8.0 (6.5, 9.6)	8.2 (6.8, 9.7)
Shrubs/Woody (%)	7.9 (6.2, 9.6)	13.0 (10.6, 15.3)
Pine BA (ft^2/acre)	32.4 (29.0, 35.8)	30.0 (26.7, 33.2)
Hardwood BA (ft^2/acre)	8.3 (6.7, 9.9)	14.6 (12.5, 16.8)

Chapter 2: Assessing landscape factors associated with the decline of the southeastern pocket gopher (*Geomys pinetis*), a native ecosystem engineer

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Abstract

Identifying and restoring habitat are vital steps in planning the recovery of a threatened species. Determining local habitat characteristics are important; however, some local habitats are unable to sustain populations due to landscape factors such as distance to the nearest suitable patch or density of dispersal barriers. Determining these landscape factors is vital in allowing organisms of conservation concern to persist. My objective was to use the southeastern pocket gopher (*Geomys pinetis*) as a model organism for exploring landscape factors that may influence species decline. To assess this objective, I identified a set of historically occupied sites, and then determined which sites had recent re-surveys at 3 spatial scales, $1km^2$, $2km^2$, and $4km^2$. I then gathered variables related to land cover, canopy cover, soil, and fragmentation. For the $1km^2$ scale, the agriculture model was the best model to explain *G. pinetis* persistence. At the $2km^2$ scale, both agriculture and urbanization influenced persistence of *G. pinetis*. At the $4km^2$ scale, the global model, which included variables relating to fragmentation, urbanization, agriculture, soil, and habitat loss, was the top model. Future conservation of *G. pinetis* should consider both local habitat variables and landscape variables as both scales are important for persistence.

Introduction

Identifying and restoring habitat are vital steps in planning the recovery of a threatened species (Griffith et al. 1989, Nagendra et al. 2013). Local habitat variables such as basal area, food availability, and soil moisture are all important considerations when determining species requirements (Huxel and Hastings 1999). However, some restored areas with suitable local habitat are unable to sustain populations due to variables in the surrounding landscape, such as long distances to the nearest habitat patch, unavailability of habitat patches, and high density of dispersal barriers like roads (Araújo and Williams 2000, Coppeto et al. 2006, Stephens and Anderson 2014). Determining these landscape factors is important for establishing conservation areas that will allow species persistence (Araújo and Williams 2000, Mac Nally and Horrocks 2002).

The southeastern pocket gopher (*Geomys pinetis*) is a model organism for examining underlying landscape factors of species decline as it is a fossorial rodent that has experienced marked declines and is of conservation concern throughout its historic range (Figure 2.1), (Alabama Department of Conservation and Natural Resource 2015, Florida Fish and Wildlife Conservation Commission 2012, Ozier 2010). Factors responsible for *G. pinetis*'s decline are anecdotal but assumed to be due to changes in natural pinelands, especially longleaf pine (*Pinus palustrus*), such as conversion to agriculture, loss of suitable habitat, and urbanization (van Lear and Harlow 2002, Southern Wildlife Consultants 2008). These landscape factors have been shown to affect other species in the region such as the gopher tortoise (*Gopherus polyphemus*) (Auffenberg and Franz 1982).

With populations still declining, *G. pinetis* are of conservation interest because of the benefits they provide to ecosystems. As ecosystem engineers, they create tunnels and burrows which affect ecosystem services such as water filtration, nutrient cycling, and soil aeration (Kalisz and Stone 1984, Jones et al. 1994, Forbis et al. 2002, Reichman and Seabloom 2002). Additionally, the tunnel systems provide habitat for several commensals, some which are federally listed such as the gopher frog (*Lithobates capito*) and the eastern indigo snake (*Drymarchon couperi*) (Blihovde 2006, Miller et al. 2012). While *G. pinetis* populations are thriving in some areas, other areas that historically supported populations have not had *G. pinetis* present for decades (Guyer et al. 2007). Additional surveys have shown apparent declines across the range, even in areas that previously supported robust populations (Guyer et al. 2007, Southern Wildlife Consults 2008).

Due to the benefits *G. pinetis* provide, vegetation and soil factors that provide local suitable habitat have been the focus of a number of recent studies (Warren et al. 2017a, Warren et al. 2017, Bennett 2018). These studies suggest that *G. pinetis* prefer areas with sandy soils (Warren et al. 2017a, Bennett 2018) and that *G. pinetis* occupancy is positively related to intermediate levels of canopy cover (Bennett 2018). While these studies provided important information for local habitat variables to conserve and restore, questions remain regarding causes of declines across the landscape.

Due to uncertainties about landscape factors affecting *G. pinetis* persistence, my objective was to quantify persistence using historic and current surveys. I hypothesized that decreasing amounts of habitat and suitable soils, would decrease the likelihood of *G. pinetis* persistence (Araújo and Williams 2000). This prediction is based on declines that occurred with Mazama pocket gophers (*Thomomys mazama*) due to encroachment of invasive plants and changes in fire interval (Stinton 2005) and the selection of sandy soils by *G. pinetis* (Warren et al. 2017a, Bennett 2018). Additionally, increases in fragmentation, urbanization, and agriculture would decrease the likelihood of *G. pinetis* persistence (Table 2.1). Anecdotal evidence suggests that *G. pinetis* is poor at dispersing across roads and is absent from urban centers; thus, I predicted that increases in urbanization and fragmentation would decrease the probability of persistence (Warren personal communication). I also predicted *G. pinetis* persistence would decrease with increasing amounts of agriculture due to the agriculture practices in the region which include tilling and disking top soil (Katsvairo et al. 2006).

Methods

Site Selection

Within the historic range, I selected study sites from two studies of recent *G. pinetis* occurrence in historically occupied sites (Figure 2.1). Southern Wildlife Consults (2006) resurveyed historic locations in Georgia during June-August 2006, performing roadside surveys of historic locations (Table 2.2) and georeferening *G. pinetis* mounds seen with a 1 km search radius of historic sites. They considered mounds independent if they were > 0.5 km from other mound locations (Southern Wildlife Consults 2008). Barbour et al. (2015) surveyed historic locations in Alabama in 2014-2015 (Table 2.2).

I identified a set of historically occupied sites, and then determined which sites had recent re-surveys that fell within a 2km buffer of the historically occupied location via GIS (ESRI 2015). To capture changes in the surrounding landscape that may be important for *G. pinetis*, I chose 3 spatial scales: 1km^2, 2km^2, and 4 km^2. Within a GIS, I first made a circular buffer zone at all three radiuses: 500 m, 1000 m, and 2000 m. Then, I created an envelope around each of the circular buffers to create square buffers with the following areas: 100 ha, 400 ha, and 1,600 ha.

For a resurvey site to be selected in that spatial scale, the resurvey site needed to fall within the square buffer zone of the historic location.

Variable Selection

I gathered variables related to land cover, canopy cover, soil, and fragmentation at each spatial scale. I used land cover and canopy cover data from the Multi-Resolution Land Characteristics Consortium (i.e. NLCD) (Homer et al. 2015, U.S. Forest Service 2016). As non-forested cover types by definition have low canopy cover, I did not calculate cover for those classes. I reclassified canopy cover values into low, medium, and high categories for each of the forest classes in the NLCD dataset based on trends in occupancy for *G. pinetis* observed in the previous chapter (Deciduous, Evergreen, and Mixed forests) (Homer et al. 2015) (Table 2.3). I then calculated the area of each cover class for each site.

To future explore the effects urbanization intensity, I divided the development categories within NLCD. I calculated the area of each development class within NLCD which are based on the amount of impervious surface (Table 2.4).

For soil information, I downloaded gridded Soil Survey Geographic Database (gSSURGO) information for Alabama and Georgia (Soil Survey Staff). I extracted soil texture data for each site at all three spatial scales and then calculated the area occupied by each texture class. Due to the large number of texture classes (*n* = 26), I reclassified texture classes as highly suitable, suitable, or unsuitable following previous evaluations of the species (Table 2.5) (Bennett 2018, Warren et al. 2017a).

I assessed the density of roads for study sites using the TIGER/Line Primary and Secondary road datasets (U.S. Census Bureau 2016). I included primary roads, which are highways within the interstate system, and secondary roads, which included city streets, county roads, and state highways, for each county where locations had been documented (U.S. Census Bureau 2016). I then calculated the length of road in meters for each study site and divided by the area of the site to get the length of road per hectare.

I calculated indices of fragmentation and using FRAGSTATS (McGarigal and Marks 1995). First, I reclassified the original NLCD raster data into suitable habitat and unsuitable habitat (Table 2.6) (Bennett 2018, Warren et al. 2017b). Using QGIS, I split the reclassified raster file into individual sites and saved them as graphics (QGIS Development Team 2019). I then batch processed the sites in FRAGSTATS to quantify largest patch size and patch density (McGarigal et al. 2012).

Data Analysis

Before creating candidate models, I evaluated variables for correlation using the *car* package in program R (Fox and Weisberg 2011, R Core Team 2019). For collinear variables, I selected the one that was more biologically relevant. For each spatial scale, I evaluated the same set of models based on *a priori* hypotheses about whether *G. pinetis* persistence was linked to variables of habitat loss, fragmentation, urbanization, agriculture, or soil (Table 2.1).

At each spatial scale, I modeled species persistence with logistic regression. I compared the models using Akaike's Information Criterion adjusted for small sample sizes (AICc), where the most parsimonious model has the lowest AICc value (Akaike 1998, Anderson and Burnham 2002). I evaluated model fit using the concordance statistic (c-statistic) (Austin and Steyerberg 2014). I considered models 2 AICc units as competing models.

I further assessed the relationship between urbanization and *G. pinetis* persistence by creating a subset of individual development intensity models based on the NLCD development classes. Because there was a gradient of development classes included in the urbanization for the full model, I wanted to know the relative importance of varying intensities in relation to *G. pinetis* persistence. I also compared those models using AICc (Akaike 1998, Anderson and Burnham 2002). I performed all analyses in R (R Core Team 2019).

Results

I identified 519 historically occupied sites with re-surveys throughout Alabama (*n* = 135) and Georgia (*n* = 384) (Figure 2.1). In Alabama, 30 (22.2%) resurveyed sites had *G. pinetis*, and Georgia had 106 (27.6%) sites.

At the 1 km^2 scale, the agriculture model, which included the percentage of cultivated crops as land cover, was the top model explaining *G. pinetis* persistence (Table 2.7). For every 1% increase of cultivated crops as land cover, a site was 1.04 (1.02, 1.06, 95% C.L.) times as likely to have *G. pinetis* present. The concordance statistic indicated reasonable predictive ability of the agriculture model (C=0.667) (Austin and Steyerberg 2012). For the additional assessment of individual development categories, high intensity development was the best univariate development model (Table 2.8).

The urbanization model and the agriculture model were both competing models (within 2 ΔAICc units) for the 2 km^2 scale (Table 2.9). The best model was the urbanization model, which included the percentage of all types of development intensities as land cover. For every 1% increase in developed land cover, a site was 1.05 (1.01, 1.09, 95% C.L.) times less likely to have *G. pinetis* persistence. The next best model was the agriculture model which included percentage of cultivated crops as land cover (Table 2.9). For every 1% increase in cultivated crops as land cover, a site was 1.04 (1.01, 1.06, 95% C.L.) times more likely to have *G. pinetis* present. The concordance statistic indicated mediocre and reasonable predictive ability of both the urbanization and agriculture model (C = 0.593 and 0.662, respectively) (Austin and Steyerberg 2012).

In post hoc evaluation of the individual development categories at the 2 km^2 scale, high intensity development was the top model (Table 2.10). For every 1% increase in high intensity development as land cover, a site is 9.2 (0.77, 111.72, 95% C.L.) times less likely to have *G. pinetis* persist.

For the 4 km^2 scale, the global model best explained *G. pinetis* persistence (Table 2.11). For fragmentation, at an increase of 1 patch per 100 hectares, a site is 1.01 (1.0, 1.03, 95% C.L.) times as likely to have *G. pinetis* persist. A site was 1.03 (0.98, 1.08, 95% C.L.) times less likely to have *G. pinetis* persist for every 1% increase in developed land cover. There was no conclusive relationship with amount of habitat. For every 1% increase in habitat, a site was 1.00 (0.97, 1.03, 95% C.L.) times as likely to have *G. pinetis* present. For the agriculture model, there was a positive effect; for every 1% increase in cultivated crops, a site was 1.04 (1.00, 1.08, 95% C.L.) times as likely to have *G. pinetis* persist. There was also a positive relationship between the amount of suitable soil and *G. pinetis* persistence; for every 1% increase in suitable soil, a site is 1.02 (0.99, 1.06, 95% C.L.) times more likely to still support *G. pinetis*. The concordance statistic indicated good predictive ability of the global model (C=0.713) (Austin and Steyerberg 2012).

After separating the development categories, the top models were high intensity development and medium intensity development. However, all models had negative relationships between *G. pinetis* persistence and development (Table 2.12). For every 1% increase in high intensity development as land cover, a site was 2.83 (1.04, 7.69, 95% C.L.) times less likely to have *G. pinetis* still present. For every 1% increase in medium intensity development as land cover, a site is 1.39 (1.05, 1.84, 95% C.L.) times less likely to have *G. pinetis* persist.

Discussion

At all three spatial scales, my hypothesis that declines in habitat would decrease the probability of *G. pinetis* was not supported. While habitat loss was included in the global model at the largest scale, there was no conclusive relationship with persistence (Table 2.11). However, loss of habitat, especially longleaf pine forest, has anecdotally been one of the leading factors for decline in *G. pinetis* (Avise and Laerm 1982, Gates and Tanner 1988, Warren et al. 2017a, Warren et al. 2017b). Loss of habitat is likely important for *G. pinetis* persistence, but the variables used may not have been measured at sufficiently fine spatial resolution to capture a relationship. All of the data used to produce the habitat layer, a combination of land cover, canopy cover, and soil data, was available at a 30m spatial resolution (Homer et al. 2015, Soil Survey Staff, US Forest Service 2016). Additionally, the land cover categories classified as suitable (Table 2.6) were likely too general to capture categories important to *G. pinetis* persistence.

Similar problems may have been encountered with the data used for suitable soils. My hypothesis that increases in the amount of suitable soil would increase *G. pinetis* persistence was only supported at the largest scale (4 km^2) (Table 2.11). While previous studies have found soil characteristics to be strong predictors of *G. pinetis* occupancy, (Warren et al. 2017a, Bennett 2018), the coarse spatial resolution (30m) of gSSURGO data is likely a poor predictor for persistence (Soil Survey Staff). At the smaller spatial scales, there was little variation in availability of suitable soils so almost all of the site area was classified as suitable. While soil characteristics are important for *G. pinetis* presence, soil formation takes thousands of years

(Wakatsuki and Rasyidin 1992, Stockmann et al. 2014) so differences in soil texture between historic and current surveys was likely negligible.

The hypothesis that increased fragmentation would decreased the probability of *G. pinetis* persistence was not supported at any of the spatial scales. Fragmentation was included in the global model for the 4 km^2 scale but contrary to my hypothesis, suggested a slight positive effect of fragmentation on persistence. The positive effect may be due to the survey data locations, which were collected using roadside surveys (Southern Wildlife Consults 2008), and the reclassification of land cover and soils excluded roadways as habitat. Fragmentation, particularly by roads, has been shown to negatively impact small mammals by creating barriers to dispersal (Ascensão et al. 2016, Gerlach and Musolf 2001, McGregor et al. 2008). Roads create an additional underground barrier for fossorial mammals through soil compaction (Esperandio et al. 2019). Additionally, as with the habitat loss and soil models, finer scale classification of habitat and soil by site would likely be better indicators of persistence.

My hypothesis that increases in urbanization would decrease the probability of persistence was supported at the 2 km^2 and 4 km^2 scale. While the 1 km^2 spatial scale urbanization model was not a top model, there were no persistence sites with high intensity urbanization at that spatial scale. After sub-setting the urbanization data into intensity classes, high intensity followed by medium intensity development had the strongest negative effects on *G. pinetis* persistence. The intensity classes were constructed based on percentages of impervious surface (Table 2.4) and amount nighttime light imagery which include areas such as apartment complexes and single-family homes (Homer et al. 2015, Xian and Homer 2010). Evidence in other pocket gopher species suggests these areas are problematic to persistence as impervious surface creates a barrier to underground movement (Hansler et al. 2017, Stinton 2005).

There were also negative effects for open and low intensity development. *G. pinetis* have been located along roadsides, in golf courses, and on managed lawns in the past, which are considered open and low intensity development (Avise and Laerm 1982, Homer et al. 2015). Other species of gophers are seen as pests in those areas due to their surface mounds and tunneling (Baldwin et al. 2013, Hansler et al. 2017). While these categories have lower amounts of impervious surface, they still negatively impacted *G. pinetis* persistence. This may be due to increases in human populations where *G. pinetis* are considered as nuisance animals and removed. Additionally, these areas occur in or near areas with intense urbanization which have greater negative effects on persistence.

My hypothesis that *G. pinetis* persistence would decrease with increasing amounts of agriculture in the form of cultivated crops was not supported at any spatial scale. At both the 1 km^2 scale and the 2 km^2 scale, there was a positive effect of increasing cultivated crops as ground cover and *G. pinetis* persistence (Table 2.7, 2.9). A similar trend was observed in the global model at the 4 km^2 scale (Table 2.11). Survey locations in the cultivated crop category were primarily located in the road margins near agriculture fields, but the survey sites were generated using buffers that captured the cultivated crops in the area. The Cropland Data Layer (United State Department of Agriculture 2018) suggested the main crops surrounding *G. pinetis* locations were peanuts, cotton, and corn in both Alabama and Georgia (USDA 2018).

While crops may be used as forage for *G. pinetis* (Mayo 2018), it is unlikely the home range would be centered in the cultivated fields due to agriculture practices such as conventional tillage and harvest which would damage tunnel systems (Katsvairo et al. 2006, Raper et al. 2000). However, changes in tillage regime for many crops in the Southeast may cause less damage to *G. pinetis* tunnels due to minimal surface and soil disturbance (Katsvairo et al. 2006).

This conservation tillage and mixed rotation with native perennial grasses may make cultivated crops more attractive to *G. pinetis* herbivory (Katsvairo et al. 2006). In other pocket gopher species, herbivory of crops has been a primary concern of landowners and a prominent justification for lethal management (Hansler et al. 2017, Stinton 2005, Williams and Cameron 1986).

Probability of *G. pinetis* persistence was related to landscape variables at several scales in Georgia and Alabama. While some variables were redundant and too coarse spatially, they still offered valuable information on potential threats to *G. pinetis* persistence at a landscape scale. Increasing urbanization and conversion to agriculture may have mixed effects on *G. pinetis* persistence. Urbanization, even at low intensities, will likely be detrimental to populations by limiting dispersal and foraging opportunities resulting from increasing soil compaction and creation of impervious surfaces (Ascensão et al. 2016, Gerlach and Musolf 2001). Agriculture, depending on the crop and farming practices, may provide *G. pinetis* with food resources or a corridor to disperse to suitable soils and cover.

These persistence models, based on limited survey data, can be used to inform conservation decisions. Survey locations, with a concentration on natural areas, coupled with historic land use and land cover change may offer more insight on specific types of change responsible for declines in *G. pinetis* in otherwise available habitat. The additional of historic data at finer scales would be beneficial to future planning of translocation sites or conservation areas.

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Tables and Figures

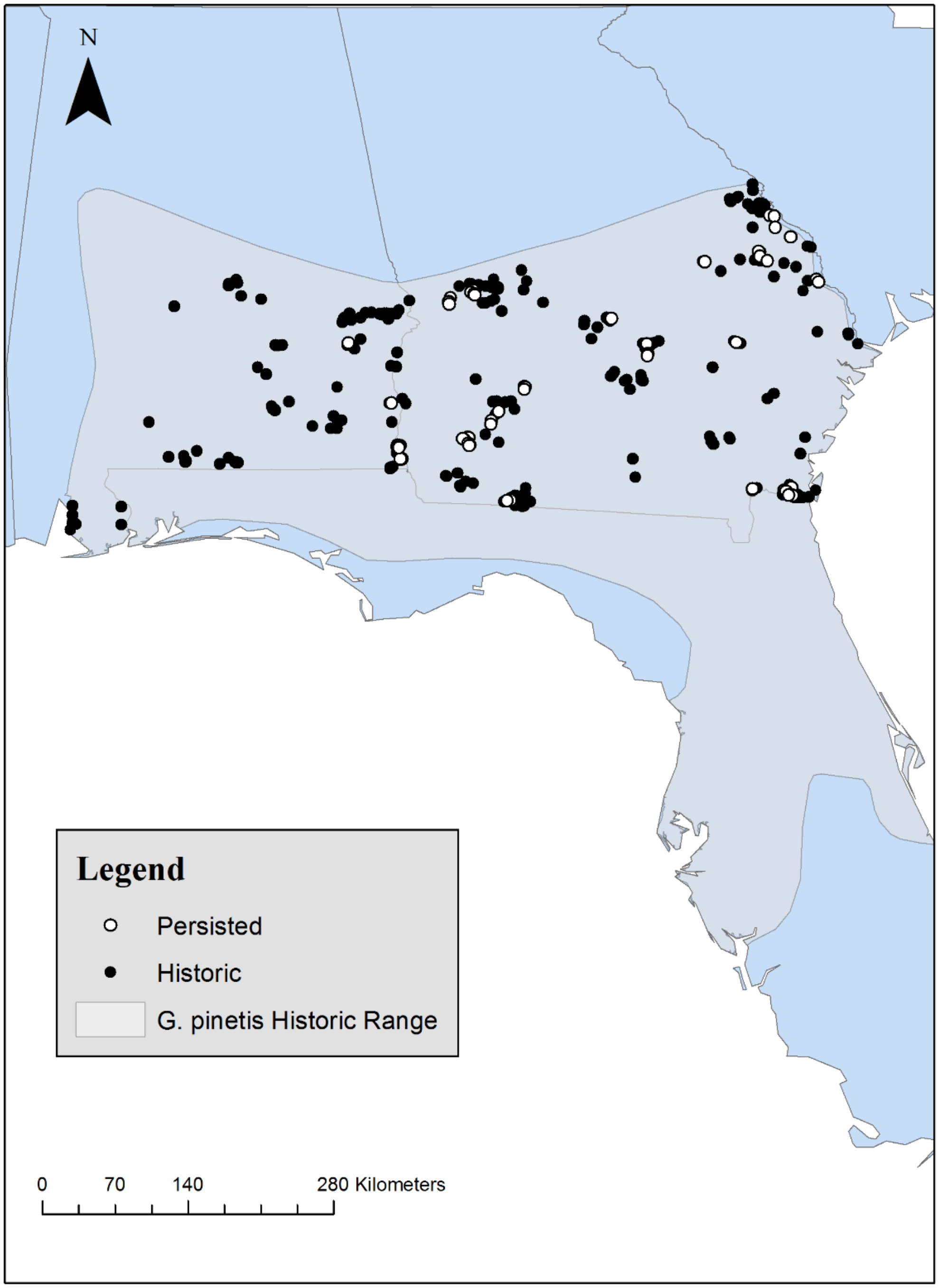

Figure 2.1: Mapped locations of surveys from 2006 and 2014-2015 within *G. pinetis* historic range (light grey). The black points indicate historic sites of *G. pinetis*; whereas, white points were resurveyed sites where *G. pinetis* has persisted.

Table 2.1. Hypotheses for the relationships between variables and *G. pinetis* persistence

Model	Variables	Prediction
Habitat Loss	Suitable Soil + Suitable Cover	With decreasing percentages of suitable cover and suitable soil, *G. pinetis* persistence will decrease
Fragmentation	Patch Density	With increasing fragmentation of habitat (increasing patch density), *G. pinetis* persistence will decrease
Urbanization	Developed (Open, Low, Medium, High)	With increasing percentages of developed land covers, *G. pinetis* persistence will decrease
Agriculture	Cultivated Crops	With increasing percentages of cultivated crops as land cover, *G. pinetis* persistence will decrease
Soil	Suitable Soil	With increasing amounts of suitable soil, *G. pinetis* persistence will increase

Table 2.2. Sources of historic *G. pinetis* locations from studies in Georgia and Alabama on current occupancy of *G. pinetis*

Study	Source of Historic Locations
Southern Wildlife Consults	Florida State Collection of Arthropods
Michael Barbour	Field Museum of Natural History Smithsonian National Museum of Natural History University of Michigan Museum of Zoology Kansas University Mammal Collection

Table 2.3. Classification of canopy cover from National Land Cover Database Canopy Cover layer

Reclassification	Original Canopy Cover (%)
High	75-100
Medium	26-74
Low	0-25

Table 2.4. Percentages of impervious surface for development intensities in the National Land Cover Database

Development Intensity	% Impervious Surface	Example
Open Space	0-20	Parks, golf courses, large-lot single-family houses
Low Intensity	20-49	Single-family housing units
Medium Intensity	50-79	Single-family housing units
High Intensity	80-100	Apartment complexes, commercial or industrial lots

Table 2.5. Suitability classifications for *G. pinetis* based on original gridded SSURGO texture classes

Reclassification	Original Texture Class
Highly Suitable	Fine sand Fine sandy loam Loam Loamy coarse sand Loamy fine sand Loamy sand Sand Sandy loam Silt loam
Suitable	Coarse sand Coarse sandy loam Gravelly coarse sand Gravelly fine sandy loam Very fine sandy loam
Unsuitable	No data available Bedrock Clay Clay loam Muck Mucky fine sand Mucky peat Paragravelly sandy clay loam Sandy clay Sandy clay loam Silty clay Silty clay loam

Table 2.6. Habitat classification for *G. pinetis* based on National Land Cover Database 2011 cover classes

Reclassification	**Original NLCD Cover Class**
Suitable	Evergreen Forest Mixed Forest Shrub/Scrub Grassland/Herbaceous Pasture/Hay
Unsuitable	Open Water Perennial Ice/Snow Developed, Open Space Developed, Low Intensity Developed, Medium Intensity Developed, High Intensity Barren Land (Rock/Sand/Clay) Deciduous Forest Cultivated Crops Woody Wetlands Emergent Herbaceous Wetlands

Table 2.7. 1 km^2 scale model suite selection for landscape variable influencing *G. pinetis* persistence at sites (n = 410) in Alabama and Georgia.

Model	**Parameters**	**AICc**	**ΔAICc**	**w_i**
Agriculture	2	187.7	0	0.7
Global Model	6	190.0	2.3	0.2
Urbanization	2	192.3	4.6	0.1
Intercept Only	1	195.7	8.0	0.0
Soil	2	196.8	9.1	0.0
Fragmentation	2	197.1	9.4	0.0
Habitat Loss	2	197.1	9.8	0.0

Table 2.8. 1 km^2 scale model suite selection for development categories as land cover influencing *G. pinetis* persistence at sites (n = 410) in Alabama and Georgia.

Model	**Parameters**	**AICc**	**ΔAICc**	**w_i**
High Intensity Development	2	182.5	0	0.9
Medium Intensity Development	2	187.1	4.6	0.1
All Development Combined	2	192.3	9.8	0.0
Low Intensity Development	2	194.3	11.8	0.0
Open Development	2	195.2	12.7	0.0
Intercept Only	1	195.7	13.3	0.0

Table 2.9. 2 km^2 scale model suite selection for landscape variables influencing *G. pinetis* persistence at sites (n = 432) in Alabama and Georgia.

Model	**Parameters**	**AICc**	**ΔAICc**	**w_i**
Urbanization	2	294.3	0	0.6
Agriculture	2	296.2	1.9	0.2
Global Model	6	296.7	2.4	0.2
Intercept Only	1	303.4	9.1	0.0
Habitat Loss	2	304.8	10.5	0.0
Soil	2	305.1	10.7	0.0
Fragmentation	2	305.3	10.9	0.0

Table 2.10. 2 km^2 scale model suite selection for development categories as land cover influencing *G. pinetis* persistence at sites (n = 432) in Alabama and Georgia.

Model	**Parameters**	**AICc**	**ΔAICc**	**w_i**
High Intensity Development	2	289.9	0	0.7
Medium Intensity Development	2	292.2	2.3	0.2
All Development Combined	2	294.3	4.4	0.1
Open Development	2	296.1	6.1	0.0
Low Intensity Development	2	298.2	8.3	0.0
Intercept Only	1	303.4	13.5	0.0

Table 2.11. 4 km^2 scale model suite selection for landscape variables influencing *G. pinetis* persistence at sites (n = 450) in Alabama and Georgia.

Model	**Parameters**	**AICc**	**ΔAICc**	**w_i**
Global Model	6	363.9	0	0.8
Agriculture	2	367.5	3.6	0.1
Urbanization	2	369.9	6.0	0.0
Fragmentation	2	376.1	12.2	0.0
Intercept Only	1	377.2	13.3	0.0
Soil	2	377.9	14.0	0.0
Habitat Loss	2	378.6	14.7	0.0

Table 2.12. 4 km^2 scale model suite selection for development categories as land cover influencing *G. pinetis* persistence at sites (n = 450) in Alabama and Georgia.

Model	**Parameters**	**AICc**	**ΔAICc**	**w_i**
High Intensity Development	2	367.0	0	0.5
Medium Intensity Development	2	368.4	1.1	0.3
All Development Combined	2	369.9	2.6	0.1
Low Intensity Development	2	371.0	3.8	0.1
Open Development	2	372.0	4.8	0.0
Intercept Only	1	377.2	9.9	0.0

Appendix

Mean (95% confidence interval) for the **1 km^2 scale** landscape variables across 410 sites

Variable	**Persisted (n=26)**	**Extirpated (n=384)**
Barren (%)	0.66 (-0.14, 1.45)	0.48 (0.21, 0.74)
Crops (%)	16.96 (9.1, 24.81)	7.39 (6.18, 8.59)
Deciduous Forest, low canopy (%)	0.56 (0.31, 0.80)	0.31 (0.25, 0.37)
Deciduous Forest, medium canopy (%)	5.83 (3.47, 8.20)	3.08 (2.60, 3.55)
Deciduous Forest, high canopy (%)	5.28 (2.57, 8.00)	6.54 (5.57, 7.51)
Evergreen Forest, low canopy (%)	0.93 (0.39, 1.47)	0.74 (0.61, 0.87)
Evergreen Forest, medium canopy (%)	8.75 (5.75, 11.75)	6.98 (6.21, 7.74)
Evergreen Forest, high canopy (%)	11.82 (7.28, 16.36)	13.15 (11.89, 14.41)
Mixed Forest, low canopy (%)	0.92 (0.04, 0.15)	0.09 (0.07, 0.11)
Mixed Forest, medium canopy (%)	2.08 (0.92, 3.24)	1.38 (1.11, 1.65)
Mixed Forest, high canopy (%)	3.18 (1.80, 4.56)	3.64 (3.20, 4.08)
Developed, open (%)	8.63 (6.71, 10.54)	11.14 (10.28, 12.00)
Developed, low (%)	3.78 (1.74, 5.81)	6.71 (5.75, 7.67)
Developed, medium (%)	0.24 (0.07, 0.41)	2.54 (1.93, 3.15)
Developed, high (%)	0 (None in category)	1.30 (0.81, 1.80)
Developed, all (%)	12.65 (8.98, 16.32)	21.69 (19.36, 24.03)
Grasslands (%)	9.05 (6.53, 11.56)	6.95 (6.03, 7.87)
Open Water (%)	0.37 (-0.11, 0.85)	0.67 (0.47, 0.87)
Pasture (%)	5.54 (3.00, 8.07)	5.37 (4.53, 6.21)
Shrub/Scrub (%)	9.50 (5.29, 13.71)	10.70 (9.61, 11.78)
Emergent Herbaceous Wetland (%)	0.76 (0.32, 1.21)	1.41 (1.03, 7.80)
Woody Wetlands (%)	6.00 (2.67, 9.33)	9.44 (8.14, 10.74)
Roads (m/ha)	39.44 (30.71, 48.18)	52.66 (48.07, 57.26)
Suitable Soils (%)	86.86 (79.74, 93.98)	82.94 (80.82, 85.06)
Unsuitable Soils (%)	13.14 (6.02, 20.26)	17.06 (14.94, 19.18)
Patch Density	408.58 (405.71, 411.44)	407.40 (406.71, 408.10)
Largest Patch Index	14.62 (12.72, 16.53)	14.303 (13.81, 14.79)
Suitable Cover, Suitable Soil (%)	44.22 (36.23, 52.21)	41.88 (39.70, 44.05)
Suitable Cover, Unsuitable Soil (%)	6.85 (2.72, 10.98)	7.16 (6.09, 8.24)
Unsuitable Cover, Suitable Soil (%)	42.72 (33.12, 52.31)	41.09 (39.90, 43.27)
Unsuitable Cover, Unsuitable Soil (%)	6.21 (2.41, 10.02)	9.87 (8.27, 11.47)

Mean (95% confidence interval) for the **2 km^2 scale** landscape variables across 432 sites

Variable	**Persisted (n=48)**	**Extirpated (n=384)**
Barren (%)	1.07 (0.09, 2.05)	0.57 (0.33, 0.81)
Crops (%)	12.79 (9.36, 16.22)	7.45 (6.42, 8.49)
Deciduous Forest, low canopy (%)	0.53 (0.34, 0.72)	0.32 (0.26, 0.37)
Deciduous Forest, medium canopy (%)	5.26 (3.76, 6.76)	3.09 (2.66, 3.53)
Deciduous Forest, high canopy (%)	4.25 (2.76, 5.75)	7.10 (6.16, 8.04)
Evergreen Forest, low canopy (%)	0.87 (0.51, 1.22)	0.75 (0.65, 0.85)
Evergreen Forest, medium canopy (%)	7.96 (6.24, 9.67)	6.90 (6.23, 7.57)
Evergreen Forest, high canopy (%)	15.52 (12.08, 18.96)	14.75 (13.65, 15.85)
Mixed Forest, low canopy (%)	0.12 (0.07, 0.16)	0.09 (0.08, 0.10)
Mixed Forest, medium canopy (%)	2.87 (0.92, 3.24)	1.29 (1.07, 1.50)
Mixed Forest, high canopy (%)	2.50 (1.84, 3.17)	3.64 (3.20, 4.08)
Developed, open (%)	6.09 (5.12, 7.05)	8.97 (8.22, 9.72)
Developed, low (%)	2.56 (1.56, 3.56)	5.15 (4.33, 5.98)
Developed, medium (%)	0.32 (0.15, 0.49)	1.77 (1.35, 2.19)
Developed, high (%)	0.03 (0.00, 0.06)	0.82 (0.53, 1.10)
Developed, all (%)	9.00 (7.01, 10.98)	16.71 (14.73, 18.70)
Grasslands (%)	9.77 (7.40, 12.14)	7.28 (6.46, 8.10)
Open Water (%)	0.60 (0.37, 0.83)	1.02 (0.75, 1.30)
Pasture (%)	5.34 (3.84, 6.83)	5.26 (4.63, 5.89)
Shrub/Scrub (%)	9.53 (7.26, 11.79)	10.76 (9.88, 11.65)
Emergent Herbaceous Wetland (%)	2.08 (1.11, 3.05)	1.52 (1.21, 1.83)
Woody Wetlands (%)	11.23 (8.18, 14.28)	11.27 (10.03, 12.51)
Roads (m/ha)	28.43 (24.56, 32.29)	39.10 (35.77, 42.42)
Suitable Soils (%)	84.03 (78.15, 89.92)	82.34 (80.46, 84.22)
Unsuitable Soils (%)	15.97 (10.08, 21.85)	17.66 (15.78, 19.54)
Patch Density	114.16 (109.6, 118.68)	115.00 (113.60, 116.39)
Largest Patch Index	14.62 (12.72, 16.53)	21.78 (20.82, 22.74)
Suitable Cover, Suitable Soil (%)	45.71 (41.11, 50.31)	43.53 (41.61, 45.46)
Suitable Cover, Unsuitable Soil (%)	7.47 (4.71, 10.23)	7.55 (6.64, 8.46)
Unsuitable Cover, Suitable Soil (%)	38.34 (33.32, 43.35)	38.82 (36.98, 40.67)
Unsuitable Cover, Unsuitable Soil (%)	8.48 (4.95, 12.01)	10.09 (8.71, 11.48)

Mean (95% confidence interval) for the **4 km^2 scale** landscape variables across 450 sites

Variable	**Persisted (n=66)**	**Extirpated (n=384)**
Barren (%)	0.01 (0.00, 0.01)	0.01(0.00, 0.01)
Crops (%)	11.76 (9.84, 13.67)	7.61 (6.75, 8.46)
Deciduous Forest, low canopy (%)	0.58 (0.38, 0.79)	0.33 (0.27, 0.39)
Deciduous Forest, medium canopy (%)	5.18 (3.88, 6.48)	3.00 (2.62, 3.38)
Deciduous Forest, high canopy (%)	5.59 (4.22, 6.96)	7.60 (6.69, 8.51)
Evergreen Forest, low canopy (%)	0.64 (0.51, 0.77)	0.67 (0.61, 0.73)
Evergreen Forest, medium canopy (%)	7.47 (6.43, 8.51)	6.87 (6.31, 7.43)
Evergreen Forest, high canopy (%)	15.92 (13.63, 18.22)	15.70 (14.72, 16.69)
Mixed Forest, low canopy (%)	0.10 (0.08, 0.12)	0.08 (0.07, 0.09)
Mixed Forest, medium canopy (%)	1.34 (1.02, 1.66)	1.25 (1.06, 1.43)
Mixed Forest, high canopy (%)	2.77 (2.11, 3.43)	4.02 (3.65, 4.39)
Developed, open (%)	5.44 (4.54, 6.34)	7.26 (6.67, 7.86)
Developed, low (%)	2.05 (1.42, 2.69)	3.98 (3.31, 4.65)
Developed, medium (%)	0.395 (0.187, 0.602)	1.314 (1.01, 1.62)
Developed, high (%)	0.79 (0.03, 0.13)	0.57 (0.38, 0.75)
Developed, all (%)	7.97 (6.24, 9.69)	13.12 (11.51, 14.74)
Grasslands (%)	9.09 (7.28, 10.91)	7.23 (6.52, 7.94)
Open Water (%)	0.74 (0.50, 0.98)	1.49 (1.07, 1.90)
Pasture (%)	4.92 (4.11, 5.73)	5.02 (4.56, 5.48)
Shrub/Scrub (%)	10.61 (8.96, 12.25)	10.43 (9.70, 11.17)
Emergent Herbaceous Wetland (%)	1.50 (1.03, 1.97)	2.12 (1.73, 2.51)
Woody Wetlands (%)	13.02 (10.44, 15.59)	12.87 (11.66, 14.07)
Roads (m/ha)	25.27 (22.00, 28.54)	30.66 (28.29, 33.04)
Suitable Soils (%)	83.91 (79.41, 88.40)	81.27 (79.52, 83.03)
Unsuitable Soils (%)	16.09 (11.60, 20.59)	18.73 (16.97, 20.48)
Patch Density	132.16 (124.06, 140.27)	123.92 (120.42, 127.43)
Largest Patch Index	49.32 (48.98, 49.66)	50.25 (49.94, 50.56)
Suitable Cover, Suitable Soil	45.55 (42.449, 48.62)	43.83 (42.11, 45.55)
Suitable Cover, Unsuitable Soil	7.33 (5.22, 9.44)	4.72 (6.91, 8.54)
Unsuitable Cover, Suitable Soil	38.37 (34.93, 41.81)	37.45 (35.93, 38.97)
Unsuitable Cover, Unsuitable Soil	8.75 (5.99, 11.52)	11.00 (9.69, 12.31)