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A landscape genetic analysis of swamp rabbits (*Sylvilagus aquaticus*) suggests forest canopy cover enhances gene flow in an agricultural matrix

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1 **A landscape genetic analysis of swamp rabbits (*Sylvilagus aquaticus*) suggests forest canopy cover**
2 **enhances gene flow in an agricultural matrix**

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Berkman, L. K., Nielsen, C. K., Roy, C. L., and Heist, E. J. A landscape genetic analysis of swamp rabbits suggests forest canopy cover enhances gene flow in an agricultural matrix.

Abstract

Habitat loss and fragmentation pose a continued and immediate threat to wildlife and create a persistent need for ecological information at the landscape scale to guide conservation efforts. Landscape features influence population connectivity for many species and genetic analyses can be employed to determine which of these features are most important. Because population connectivity through dispersal is important to the persistence of swamp rabbits (*Sylvilagus aquaticus* Bachman, 1837) at the northern edge of their range, we used a landscape genetic approach to relate gene flow to landscape features that may impact dispersal success. We tested resistance values for attributes of land cover, watercourse corridors, canopy cover, and roads, and used causal modeling and redundancy analysis to relate these representations of landscapes to genetic distance for swamp rabbits in southern Illinois, USA. Models that included canopy cover had the strongest correlations to genetic distance and were supported by our methods whereas other models were not. We concluded high tree canopy cover enhances gene flow and landscape connectivity for swamp rabbits in southern Illinois. Our study provides important empirical evidence that landscape variables may impact the habitat connectivity of swamp rabbits. Preserving dispersal routes for swamp rabbits should focus on improving canopy cover, both in bottomland and upland, to connect suitable habitat.

Key Words

Agricultural land cover; bottomland hardwood forest; canopy cover; habitat model; matrix; swamp rabbit; *Sylvilagus aquaticus*

Introduction

45 Suitable habitat is often patchily distributed on the landscape, especially for habitat specialists
46 and species of conservation concern (Hilty et al. 2006). For such patchily distributed species (e.g.,
47 metapopulations; Levins 1969), successful colonization of suitable habitat patches is critical to long term
48 population viability. The likelihood of successfully accessing and colonizing suitable habitat patches, in
49 turn, relates to factors affecting dispersal (Gustafson and Gardner 1996) and is referred to as landscape
50 connectivity (Taylor et al. 1993). Understanding and maintaining landscape connectivity (Fahrig and
51 Merriam 1994) is of paramount importance for conservation of fragmented populations and patch-
52 dependent species. Landscape connectivity will remain a high research priority in conservation as long
53 as habitat fragmentation and land use conversion continue to pose the greatest threat to global
54 biodiversity (Sala et al. 2000; Foley et al. 2005).

55 Landscape connectivity among patches is often viewed as a function of features in the matrix, the
56 portion of the landscape that is not suitable habitat (Taylor et al. 1993). The matrix interacts with
57 aspects of the life history of a focal species, most notably, a species' vagility and propensity to disperse
58 (Baum et al. 2004; Kuefler et al. 2010; Cooney et al. 2015). For example, matrix attributes may impact
59 an organism's physical ease of movement or its perceived or real mortality risk (Zeller et al. 2012),
60 thereby affecting dispersal. Matrix attributes that enhance landscape connectivity such as vegetative
61 structure for locomotion (Anderson et al. 2007), denning sites (Schwartz et al. 2009), proximity to
62 escape routes (Epps et al. 2007), preferred microclimate (Wasserman et al. 2010), and food sources
63 (Haddad 1999) may bear some similarity to those of suitable habitat (Prevedello and Vieira 2010).
64 Indeed, without better empirical knowledge of animal movement, biologists often assume that animals
65 prefer to move through the landscape features that also correspond to suitable habitat (Zeller et al. 2012).
66 However, features seemingly unrelated to suitable habitat can impact landscape connectivity as well,
67 such as anthropogenic barriers (Epps et al. 2005; Fenderson et al. 2014), corridors (Haas 1995; Haddad

68 and Tewksbury 2005) and slopes (Short Bull et al. 2011). Less intuitively, areas that are highly
69 dissimilar to suitable habitat can promote fast, straight-line movements across expanses of the matrix
70 (Long et al. 2005; Cooney et al. 2015) and conduct rather than hinder dispersal (Kuefler et al. 2010).
71 For example, species that prefer dense cover to avoid predators in their habitat may be better able to
72 detect distant habitat patches or increase movement rates through a matrix of sparse cover (Zollner and
73 Lima 2005; Cooney et al. 2015).

74 Ultimately, the factors that influence movement to sustain biological processes across the
75 landscape are of great interest for conservation. In particular, conservation efforts require knowledge of
76 dispersal and the effective exchange of organisms among habitat patches to reduce extinction risk
77 (Brown and Kodric-Brown 1977). Though the animal movements that result in dispersal are difficult to
78 study, dispersal and reproduction result in gene flow, which can be quantified. Examining the
79 relationship between gene flow and landscape attributes, known as landscape genetics (Manel et al.
80 2003), offers a way to distinguish among features presumed to be related to gene flow using
81 hypothetical resistance surfaces developed with knowledge of life history requirements, relevant suitable
82 habitat attributes, or direct observations of movement (Spear et al. 2010). This approach has provided
83 valuable methods for understanding landscape connectivity at a crucial time for biodiversity
84 conservation (Manel and Holderegger 2013).

85 Until recently, critical information regarding landscape connectivity for leporids has been largely
86 unavailable. Their movements are generally limited and notoriously difficult to observe and many
87 leporids are species of concern due to loss, degradation, and fragmentation of habitat (Smith 2008).
88 Recently, landscape genetics studies (Estes-Zumh et al. 2010; Fenderson et al. 2014) have explored
89 possible links between gene flow and landscape features for rare leporids. Landscape use can vary
90 widely even among similar species and the effect of matrix attributes may be species-specific

(Prevedello and Vieira 2010) making it difficult to extrapolate the conclusions of previous landscape genetic studies. For example, dispersal is influenced by vegetation cover for the marsh rabbit (*Sylvilagus palustris* Bachman, 1837; Forsys and Humphry 1996) but, surprisingly, not for the pygmy rabbit (*Brachylagus idahoensis* Merriam, 1891; Katzner and Parker 1998).

Like many other rare leporids, swamp rabbits (*Sylvilagus aquaticus* Bachman, 1837) are habitat specialists and are patchily distributed, especially at the northern fringe of their range (Roy Nielsen et al. 2008; Hillard et al. 2017). Swamp rabbits are native to the southeastern US and, although legally hunted in Illinois, they are endangered in Indiana (Indiana Department of Natural Resources 2015) and a species of conservation concern in Missouri (Missouri Department of Conservation 2015). Cryptic and difficult to study, swamp rabbits have received research attention due to the loss of their preferred bottomland hardwood forest habitat (Whitaker and Abrell 1986; Kjolhaug et al. 1987; Chapman and Litvaitis 2003; Crawford et al. 2012), decline in the northern part of their range (Terrel 1972; Dailey et al. 1993; Sole 1994; Barbour et al. 2001), and the recognition that sparse ecological knowledge has existed for this species (Roy Nielsen et al. 2008; Dumyahn et al. 2015). More recent studies have turned to landscape and metapopulation approaches to better understand population dynamics and effects of habitat fragmentation at the northern edge of their range (Roy Nielsen et al. 2008; Scharine et al. 2009; Scharine et al. 2011; Robinson et al. 2016). However, no studies have explicitly examined landscape connectivity of swamp rabbits using empirical data. Additionally, little prior knowledge exists from which to develop testable hypotheses regarding landscape connectivity. Those studies that have used radiotelemetry to document movements of swamp rabbits have focused on home ranges (Kjolhaug and Woolf 1988; Zollner et al. 2000b; Dumyahn and Zollner 2010; Vale and Kissell 2010; Crawford et al. 2018) and none have discerned movements associated with dispersal. Thus, the aim of our study was to

determine which landscape features are related to swamp rabbit gene flow and could influence landscape connectivity at the northern fringe of their range.

Swamp rabbit occurrence is positively related to brushy habitat, particularly the early successional structure in canopy gaps of mature bottomland hardwood forest (Zollner et al. 2000a; Vale and Kissell 2010; Scharine et al. 2009). Additionally, biologists have long recognized the association of swamp rabbits with wetland habitats (Svihla 1929; Cockrum 1949; Hunt 1959). The physical distance to water is related to swamp rabbit presence (Terrel 1972), and occupancy increases with proximity to semi-permanently flooded or intermittently exposed wetlands (Scharine et al. 2011). This connection to a water source was attributed to the predator avoidance strategy of swamp rabbits, which is escaping into water when threatened (Terrel 1972; Scharine et al. 2011). Watercourses can act as conduits for dispersal of terrestrial vertebrate species associated with aquatic or riparian habitat but this association may be due to riparian features rather than the presence of the watercourse itself (Spear et al. 2005; Vignieri 2005; Spear and Storfer 2008; Richards-Zawacki 2009). In addition to land cover in riparian zones or bottomlands, upland vegetation may also influence landscape connectivity. Studies show the use of upland areas increases during flooding (Conaway et al. 1960; Zollner et al. 2000b; Vale and Kissell 2010) and the physical contiguity of land cover types in these upland areas that receive only sporadic use influences swamp rabbit abundance (Scharine et al. 2009). Additionally, roads (Fahrig and Rytwinski 2009), agricultural, open, and developed expanses also may act as a barrier for leporids (Forys and Humprey 1996).

Without knowledge of swamp rabbit dispersal, we specified an exhaustive set of hypotheses for testing in a landscape genetic framework assuming (1) swamp rabbits disperse in areas that resemble their suitable habitat and (2) features that act as barriers for many species also influence swamp rabbit movement. We compared multiple hypothetical representations of the aforementioned landscape

features which were depicted in terms of their potential obstruction or facilitation of swamp rabbit movement (Spear et al. 2010). Features or combinations of features were then translated into resistance surfaces, hereafter “surfaces,” in a GIS and mathematically related to genetic distance. Although these landscape genetic techniques have received recent criticism and re-evaluation (e.g., Cushman et al. 2013; Guillot and Rousset 2012; Graves et al. 2013; Zeller et al. 2016), they have been heavily used in empirical studies and have directed researchers towards landscape features that may influence dispersal for many species (Storfer et al. 2010). We expected gene flow to have a negative relationship to roads and agricultural or developed land cover. We also expected gene flow to be positively related to wetland land cover, upland land cover, high canopy cover, and watercourse corridors. By exploring the relationships between landscape and successful gene flow, our study can help inform decisions regarding habitat management and conservation for the swamp rabbit. Protecting or enhancing elements within the matrix that aid dispersal may help slow further range contraction and regional extirpation of this species.

Study area

Our study area consisted of approximately 1,500 km² that included the Cache River and Bay Creek watersheds in southern Illinois (Fig. 1, Supplementary Fig. S1), which is the northernmost portion of swamp rabbit range. The Cache River and Bay Creek begin approximately 60 km north of the southernmost border of Illinois and flow south, ending in the Ohio and Mississippi Rivers (Fig. 1). Development in the mid-1900s significantly altered the land cover and hydrology of our study area and converted bottomland hardwood forest to primarily row-crop agriculture (Kruse and Groninger 2003). Beginning in the 1990s, extensive restoration to hardwood tree species occurred with the goal of restoring much of the Cache River watershed to its previously forested condition (Kruse and Groninger 2003). Sample sites for our study were selected from reforested, naturally regenerating, and mature

bottomland forest based on their potential to be occupied by swamp rabbits and over 20 years of research in this area (Kjolhaug et al. 1987; Porath 1997; Woolf and Barbour 2002; Scharine et al. 2009).

Materials and Methods

Sample collection and genetic analysis

Our study was conducted across 4 subpopulations of swamp rabbits identified in the study area (Berkman et al. 2015). All sites known to be occupied in previous surveys (Kjolhaug et al. 1987; Porath 1997; Woolf and Barbour 2002; Scharine et al. 2009) or predicted to have highly suitable habitat for swamp rabbits based on models (Robinson et al. 2016) were trapped or surveyed for fecal pellets at least once during December-March 2004-2011. We analyzed unique genotypes primarily from tissue biopsies taken from trapped rabbits ($n = 113$) captured December-March 2004-2011 (Scharine et al. 2011, Crawford et al. 2018; Institutional Animal Care and Use Committee at Southern Illinois University Carbondale protocol 06-035). Hunter harvests ($n = 13$) and a road kill ($n = 1$) collected from 2006-2011 served as additional samples. We attempted to genotype 86 fecal pellet samples from latrine logs (Scharine et al. 2009). After discarding insufficiently genotyped samples (<7 loci) and duplicate genotypes from the same individual, we included 13 unique genotypes from fecal pellet sources (Berkman et al. 2015) in our analysis.

Analyses were conducted in the Southern Illinois University Carbondale Conservation Genomics Laboratory and further details of the molecular techniques, including PCR conditions are reported in Berkman et al. (2015). For fecal pellet samples, the false allele rate ranged from 0–5% and averaged 2%; and allelic dropout errors per locus ranged from 16–42% and averaged 26%. In total, we obtained 140 unique genotypes in Illinois (Berkman et al. 2015) from 15 polymorphic microsatellite markers designed for leporids: *A10*, *A121*, *A124*, *A133*, *D118*, *D121*, *sat7*, *sat8*, *sat12*, *sat16*, *sfl006*, *sfl011*, *sfl013*, *sfl014*, and *sol28* (Rico et al. 1994; Mougél et al. 1997; Surridge et al. 1997; Estes-Zumpf et al.

2008; Berkman et al. 2009). Subpopulations of swamp rabbits in the study area were found to be in Hardy-Weinberg Equilibrium at all microsatellite loci (Berkman et al. 2015).

We calculated Rousset's a (Rousset 2000), a pairwise genetic distance, for all individuals using the program SpaGeDi (Hardy and Vekemans 2002) and related this metric to landscape resistance in a causal modeling framework (Cushman et al. 2006; Wasserman et al. 2010). Individual pairwise values of resistance were obtained from models of the landscape designed to reflect features that potentially influence genetic connectivity of swamp rabbits. Surfaces representing the 4 landscape factors we considered (land cover, canopy, watercourses, and roads) are detailed further in the following sections.

Isolation-by-distance

We created a surface in which all areas had an equal cost of dispersal and all pixels were given a resistance value of 1. This model represents a simple relationship of isolation-by-distance but may be more appropriate when using resistance surfaces in a bounded study area (Lee-Yaw et al. 2009). The equal cost surface was considered a null hypothesis against which all other surfaces were examined in a causal modeling framework (Row et al. 2010). Pairwise values of resistance among sampling locations were calculated with CIRCUITSCAPE (McRae 2006) for the equal cost and all other surfaces in this study.

Expert opinion models

We hypothesized that canopy cover, land cover, roads, and watercourse corridors influence swamp rabbit dispersal. Ultimately, these 4 factors were tested against one another in a causal modeling framework. However, as is a necessary first step in landscape genetic analyses, parameter space was first explored to find a resistance surface that best represented each factor (e.g., Wasserman et al 2010). First, attributes of canopy cover, land cover and roads were ranked using expert opinion surveys (Robinson et al. 2016) and the analytical hierarchy process (Store and Kangas 2001). Agency wildlife

biologists from within the swamp rabbit's range and university researchers familiar with swamp rabbit ecology scored the importance of each attribute (e.g., mature forest) relative to other attributes within a factor (e.g., land cover) based on presumed difficulty for swamp rabbits to traverse (Robinson et al. 2016). The pairwise scores were normalized to produce weights for each attribute and averaged across the expert surveys (Robinson et al. 2016). These types of habitat modeling procedures are common in the literature (Clevenger et al. 2002; LaRue and Nielsen 2008, 2011). Experts indicated land cover classified as open water/barren land/developed land, agriculture, 0-25% canopy cover, and highways impeded dispersal (Robinson et al. 2016; Fig. 3 therein).

Resistance surfaces were generated in ArcGIS 9.3 (Environmental Systems Research Institute, Inc., Redlands, CA) at a 30 m $\times$ 30 m pixel resolution. To translate attribute weights into resistance values, the weights derived from the expert opinion surveys were multiplied by 10, rounded to integers to be compatible with the analysis software, and assigned to each pixel based on the corresponding attribute. For the roads surface, areas that were not roads were given a background resistance value of 1. To better explore parameter space (e.g., Fenderson et al. 2014) we also squared the resistance values and tested the resulting exponential surfaces (Table 1).

Binary surfaces

We tested alternative resistance surfaces that incorporated the same attributes as above but related them in a binary fashion (e.g., Fenderson et al. 2014). We specified 3 land cover types designated in land cover data from the National Land Cover Database (NLCD; Fry et al. 2011), that may be particularly influential for swamp rabbit dispersal (Robinson et al. 2016): wetland (woody wetlands and emergent herbaceous wetlands), upland (forest, shrubland and herbaceous), and heavily modified land cover (planted/cultivated and developed). Using this prediction, we developed binary surfaces for all 3 land cover types: one in which all wetland cover types were given a low resistance value of 1 and

all other types a high resistance value of 10 (“wetland” surface), another in which all upland cover had low resistance and other land cover had high resistance (“upland” surface), and a third in which modified land covers were given a high resistance value and all other land cover a low resistance value (“disturbed” surface; Table 2). By viewing canopy cover data from the NLCD (Homer et al. 2007), most of the study area contained either high or low canopy cover with few areas of intermediate canopy. We considered a surface in which high canopy cover >50% was given a low resistance value of 1 and low canopy cover <50% was given a high resistance value of 10 (“high canopy” surface).

Finally, since highways and secondary roads may be the most impactful due to size and traffic volume we tested a surface in which highways were given a resistance value of 10 (“highway” surface) while secondary roads were given a resistance value of 1 and another surface in which both highways and secondary roads were given a resistance value of 10 (“large road” surface). We also considered exponential versions of all the binary surfaces (i.e., high resistance = 100, low resistance = 1).

Watercourse corridor surfaces

Watercourses could provide a corridor for movement due to swamp rabbit affinity for open water (Terrel 1972; Scharine et al. 2011) and not merely due to riparian vegetation. Consequently, we assessed resistance surfaces that incorporated only this variable. We examined 3 resistance surfaces intended to represent a relationship between resistance to dispersal and proximity to a watercourse. We created both a narrow (60-m) and wide (800-m) corridor around all watercourses in the study area (Online Resource 1). The narrow corridor size was chosen based on the recommendation that corridors for swamp rabbits should be >1 home range wide (Harrison 1992); the smallest average home range reported for swamp rabbits was 0.006 km² (Kjolhaug and Woolf 1988). Assuming a square home range, the minimum width of this home range would be 77 m. Since the resolution of the surfaces was 30 m × 30 m, we approximated the minimum corridor as two pixels or 60 m wide. The wide corridor size (800-m) was

determined based on the observation that swamp rabbit occupancy declined to approximately 50% at a distance of 400 m from a wetland (Scharine et al. 2011). The third resistance surface included an 800-m corridor around watercourses but excluded first-order streams. Swamp rabbits seek water sources for escape (Lowe 1958) but first-order streams may be intermittent and may not provide the water source required for swamp rabbits to avoid predators. Areas inside the buffer were given a resistance value of 1. We tested two values of resistance outside the buffer: 5 and 25.

We examined the relationship of each surface to genetic distance in a simple Mantel test (Mantel 1967). The surface with the highest Mantel correlation (Mantel r) within a factor (i.e. land cover, canopy cover, roads, and watercourses) was considered as the best representative to compete with other resistance surfaces. We then created factorial combinations of the best representative from each factor by summing the resistance values (Wasserman et al. 2010). The combination surfaces were tested with the single-factor surfaces in a causal modeling framework (Cushman et al. 2006, Wasserman et al 2010).

Causal modeling

Partial Mantel tests (Smouse et al. 1986) can produce spurious significant correlations making the most influential landscape attributes difficult to discern (Spear et al. 2005, Cushman and Landguth 2010, Guillot and Rousset 2012). To determine the most supported resistance surface among the hypothetical surfaces, we employed a model selection strategy using the 2-step causal modeling scheme of Wasserman et al. (2010). Similar to Cushman et al. (2006), the first step of this process involves a simple Mantel test of all factors followed by partial Mantel tests of each landscape model, both as causal and confounding factors, with an isolation-by-distance model (analogous to the equal cost surface) and a barrier model. We modified this scheme for use of resistances calculated with CIRCUITSCAPE (McRae 2006) as explanatory variables rather than the least cost pathways that are traditionally used. Barriers were incorporated into landscapes and examined as additional landscape resistance surfaces

(e.g., Row et al. 2010) rather than creating additional distance matrices using only barriers and regarding them as null hypotheses in addition to isolation-by-distance (e.g., Cushman et al. 2006; Wasserman et al. 2010). Consequently, the first step of causal modeling incorporated 3 diagnostic tests: (1) a simple Mantel test for all landscape surfaces, (2) a partial Mantel test with the landscape surface as the causal factor and the equal cost surface as the confounding factor, and (3) a partial Mantel test with the equal cost surface as the causal factor and the landscape surface as the confounding factor. Those surfaces that produced significant Mantel correlations for the first and second tests and non-significant correlations in the third test were considered in the second step of causal modeling.

The second step of causal modeling tested the best supported surface (designated by the strongest correlation in the first simple Mantel test) against other surfaces that met the conditions in the first step. Partial Mantel tests were conducted with the top surface as the causal factor and the alternative surfaces as confounding factors, and then the reciprocal relationship was considered in a second partial Mantel test (Wasserman et al. 2010). If the top surface remained significant after partialling the effects of the alternative surface, we considered the top surface supported. If an alternative surface was significant, even with the top surface as a confounding factor, we considered it to also be supported. All analyses were accomplished in R (The R Development Core Team 2011) with the package ECODIST (Gosslee and Urban 2007). Significance of the Mantel r value (Pearson correlation) was determined with 10,000 iterations and an alpha level of 0.05. We employed a 1-tailed test appropriate for the expected relationship of pairwise resistance to a genetic distance measure (i.e., p-values represent the probability that Mantel $r < 0$).

Mantel tests and causal modeling may not correctly identify true resistance surfaces when they are highly correlated with one another (Cushman et al. 2013; Zeller et al. 2016). To characterize the level of correlation among our surfaces, we calculated the Mantel r among the resistances from all

surfaces tested. We also examined the relative support (RS) a surface received, which is the difference between the Mantel r with a surface as causal and the Mantel r with the same surface as confounding. This metric may perform better than causal modeling (Zeller et al. 2016), so we calculated RS using the results from the first step of causal modeling.

Redundancy Analysis

Redundancy analysis (RDA) provides an alternative to Mantel tests for individual-based (rather than population-based) analyses (Legendre and Fortin 2010; Kierepka and Latch 2015). We applied RDA as implemented in MEMGENE (Galpern et al. 2014) to analyze least-cost paths calculated using our resistance models. With MEMGENE, we calculated Moran Eigenvector Maps (MEMs), representations of major spatial patterns, for the sample coordinates and for the least cost paths from the resistance surfaces. The MEMs were related to genetic distance in an RDA, applying forward selection of significant MEMs ($\alpha = 0.05$) to produce a final model. Variance was partitioned among spatial patterns identified from sample coordinates and least-cost paths, similar to a distance-based redundancy analysis (Galpern et al. 2014). We regarded models with greater R^2 than the Euclidean distance model as supported (Galpern and Peres-Neto 2015).

We also performed all of the above analyses using Loiselle's kinship coefficient (Loiselle et al. 1995) as the genetic distance measure. When Loiselle's kinship coefficient was used, the equal cost surface was significantly related to genetic distance when all other surfaces were used as the confounding factor so none of the surfaces passed the second part of the first step of causal modeling. Additionally, none of the MEMs were significant when Loiselle's kinship coefficient was used in the regression. Consequently, we only report results obtained with Rousset's a .

Results

For land cover, canopy and roads; the expert opinion values had stronger Mantel correlations than the binary representations (Fig. 2). For roads, the weights derived directly from the expert opinion scores had the strongest correlation (Mantel $r = 0.219$) and for land cover (Mantel $r = 0.266$) and canopy (Mantel $r = 0.292$), the exponentially transformed weights had the strongest Mantel correlations so these surfaces were used for the causal modeling process. For watercourses, the narrow buffer watercourse surface (60 m) with the lower contrast values (5 and 1) had the strongest correlation (Mantel $r = 0.214$) and was also used for the causal modeling process. Significant correlations ($P < 0.01$) were observed in all simple Mantel tests of the hypothesized landscape surfaces.

The relationship between the equal cost surface and genetic distance was also significant (Mantel $r = 0.204$, $P < 0.001$). All factorial surfaces were significantly correlated ($P < 0.001$) with genetic distance in simple Mantel tests (Table 3). All surfaces were also significantly correlated ($P < 0.05$) with genetic distance after accounting for physical distance in a partial Mantel test and the equal cost was not significantly correlated ($P > 0.10$) after accounting for the tested surface (Table 3). This means that all surfaces that were considered passed all diagnostic tests of the first step of causal modeling. Comparing Mantel r values among the surfaces, the combination surface of land cover and canopy cover (L + C) had the strongest correlation (Mantel r) and was considered the top surface for the second step of causal modeling.

The top surface, L + C, was not significant ($P > 0.10$) in partial Mantel tests with surfaces that incorporated canopy cover (Table 4). L + C was significantly correlated ($P < 0.01$) to genetic distance in all partial Mantel tests with surfaces that did not include canopy cover. None of the alternative surfaces were significantly correlated ($P > 0.10$) with genetic distance when the top surface was the confounding factor (Table 4). The surface with all variables included (L + R + C + W) received the highest RS. All models that included canopy cover had higher RS (> 0.23) than all other models ($<$

0.20; Table 3). Most of the factorial models were highly correlated (Mantel $r > 0.85$), but the single variable models were not highly correlated with one another (Supplemental Table S2)

The RDA calculated with MEMGENE produced regression coefficients that were highest for the surfaces C + W and R + C (Table 5). The MEMs of least cost paths generated from these surfaces had higher correlations than the Euclidean distance (i.e., the null model). Furthermore, the variation partitioned to the coordinates was relatively low ($R^2 \leq 0.0061$), compared to the null model ($R^2 = 0.0411$) which indicates the MEMs generated from the top resistance surfaces captured considerable spatial genetic variation (Galpern and Peres-Neto 2015).

Discussion

We could not identify a single landscape representation as the primary driver of swamp rabbit gene flow using a causal modeling framework. High correlations among the resistances from similar surfaces make it difficult to find support for a single model (Cushman et al. 2013; Zeller et al. 2016). However, the fact that all models that included canopy cover were supported in the second step of causal modeling, received the highest RS, and models with canopy cover were supported with the RDA strongly suggests that greater canopy cover enhances gene flow for swamp rabbits in southern Illinois. We could not resolve differences among the surfaces with Loiselle's kinship coefficient despite its similar accuracy and precision (Hardy and Vekemans 2015) to Rousset's a . We suspect that the reliance on background allele frequencies in the calculation of Loiselle's kinship may be why it produced different results from Rousset's a .

We suggest that canopy cover relates to swamp rabbit landscape connectivity by promoting habitat conditions conducive for movement and, therefore, dispersal. Other studies in the region found that canopy cover positively influences detection probability (Scharine et al. 2011) and more mature forest may be related to larger home ranges for swamp rabbits (Crawford 2014), supporting the notion

that canopy cover may increase swamp rabbit movement. For our analysis, satellite imagery was used to assess canopy cover at the 1-m scale to determine whether the ground is covered by foliage, and then amalgamated to the 30-m scale to give a value for percent canopy cover for each pixel (Huang et al. 2001). A non-forest mask was applied, thus regarding anything non-forest as having no tree canopy cover (Homer et al. 2004). This means that large tracts of agricultural land or fallow fields with no canopy cover likely had a strong negative influence on the best supported models in our study. Agricultural areas that provide no canopy cover may strongly impede movement and dispersal while upland forest and bottomland forest promote dispersal of swamp rabbits in the study area.

Most habitat studies of swamp rabbits measure canopy cover at the finer, microhabitat scale, generally within bottomland hardwood forests or adjacent uplands and distinguish between mature forest canopy cover and understory vegetation (e.g. Zollner et al. 2000a; Scharine et al. 2009; Vale and Kissel 2010; Dumyahn et al. 2015; Crawford et al. 2018). Though the methods used to develop the NLCD tree canopy cover data distinguished forest canopy from non-forest cover types (Huang et al. 2001), these methods did not distinguish early successional from mature forest and understory structure was not considered. Habitat use studies of swamp rabbits that were able to separate the influence of mature forest canopy cover from understory vegetation concluded that early successional forest and canopy gaps in mature forest that allow thick understory growth promoted swamp rabbit use (Zollner et al. 2000a; Fowler and Kissell 2007; Smyth et al. 2007; Scharine et al. 2009; Vale and Kissell 2010). However, there is also a positive relationship between canopy closure and swamp rabbit latrine sites (Zollner et al. 2000a) and detection probabilities of swamp rabbits in the northern fringe of their range (Scharine et al. 2011; but see Smyth et al. 2007). Additionally, despite a similar affinity for shrub cover, swamp rabbits use more mature forest than sympatric eastern cottontails (Crawford et al. 2018). These results and those of our study raise the possibility that canopy cover and mature forest are important for

swamp rabbits at the landscape scale, particularly at the northern fringe of the swamp rabbit range (Dumyahn et al. 2015). Distinguishing between mature forest canopy cover and dense early successional vegetation is important because results from swamp rabbit habitat studies indicate a complex and scale-dependent role for variables related to forest maturity.

We did not investigate how canopy cover promotes movement for swamp rabbits but studies of other lagomorphs suggest cover and dense vegetation afford greater security from predators as well as providing thermoregulatory benefits (Barbour and Litvaitis 1993; Katzner and Parker 1997). Generally, proximity to cover influences survival, resource use, and foraging behavior of lagomorphs (Ferron and Ouellet 1992; Barbour and Litvaitis 1993; Probert and Litvaitis 1996; Katzner and Parker 1997). The lack of predator protection in areas with no canopy cover likely restricts swamp rabbit movements to areas with cover, either in the form of dense vegetation characteristic of early successional habitat or the relatively closed canopy of mature forest. Additionally, temperature moderation provided by the canopy in hot summer months may promote movements and forays and allow for long distance dispersal to connect suitable habitat patches.

At a broader scale, the pattern of genetic structure we observed may reflect how the colonization of patchy habitat occurs at the northern edge of the swamp rabbit's range. Genetic differentiation may arise among patches due to isolation and genetic drift or, instead, patches could be repeatedly recolonized from migrants originating from populations closer to the core of the range (Eckert et al. 2008). In the latter case, differentiation may arise from a founder effect and the genetic make-up of the colonizing individuals would shape the genetic structure of the peripheral populations (Barton 2001). If random individuals from the core area colonized peripheral populations, isolation-by-distance among the peripheral populations would not be expected (Eckert et al. 2008). However strong genetic structure (Berkman et al. 2015) and isolation-by-distance found among the peripheral swamp rabbit populations

in this study support the notion that these peripheral populations are not often recolonized by migrants from the core of the range. This has important conservation implications as it implies that peripheral swamp rabbit populations will not likely be repopulated from larger, more genetically diverse core areas following patch extinction.

Most bottomland forest tracts in the northern part of the swamp rabbit range are now too small to support viable populations because land has been converted to agriculture and/or altered hydrologically. Swamp rabbits generally need >10 ha (Allen 1985; Dailey et al. 1993), but small habitat patches (< 40.5 ha) have low occupancy rates (Shiebe and Henson 2003; Roy Nielsen et al. 2008). Patch isolation also may decrease occupancy (Forys and Humphrey 1999). Though small well-connected habitat patches may allow the persistence of some species (Hilty et al 2006), patches in the northern fringe of the swamp rabbit range are not well connected as evidenced by considerable population genetic differentiation in this region (Berkman et al. 2015). In Illinois, remnant bottomland hardwood forest exists within a largely agricultural matrix (Illinois State Geological Survey 2016). However, upland forest, watercourses, and grasslands interspersed among agricultural land types create structural variability within the matrix that may differentially impact swamp rabbit dispersal and landscape connectivity.

We acknowledge several weaknesses of our study, foremost being the Mantel test. Mantel tests have been criticized for both low statistical power (Legendre and Fortin 2010) and incorrect Type I error rates resulting in potentially spurious correlations (Cushman and Landguth 2010; Guillot and Rousset 2012). The causal modeling approach we employed may overcome some of these problems (Cushman and Landguth 2010), in part due to its reliance on effect size rather than P-values to determine the top models. However, causal modeling does not prevent incorrect inference when examining highly correlated (> 0.85) models (Guillot and Rousset 2012; Cushman et al. 2013; Zeller et al. 2016). Thus, we

could not make a definitive conclusion regarding the relative influence of variables other than canopy cover on swamp rabbits. Secondly, the linear arrangement of swamp rabbit habitat shaped the spatial arrangement of samples and deviations from two-dimensional isotropic sampling have the potential to impact results, though exactly how is not well known (Segelbacher et al. 2010). However, simulations indicate linear sampling is similar to the more ideal systematic and random sampling schemes in its ability to identify landscape factors influencing gene flow (Oyler-McCance et al. 2013). Finally, conclusions from landscape genetic analyses are shown to be scale and study area dependent (Short Bull et al. 2011; Fenderson et al. 2014), meaning that other factors may be significant at broader or finer scales or in different contexts.

For example, although we did not identify roads as impactful in our study, their effect may be apparent at a finer scale. Roads can reduce or prevent movements and therefore act as a barrier for many species (Fahrig and Rytwinski 2009, Simmons et al. 2010), which may be evident in genetic data (Balkenhol and Waits 2009; Holderegger and Di Giulio 2010). Some leporids avoid highways, developed areas, and areas disturbed by roads (Forys and Humphrey 1996; 1999; Roedenbeck and Voser 2008), and rabbits are killed while crossing roads (Brockie et al. 2009; Carvalho and Mira 2011). Large highways hindered genetic connectivity for the New England cottontail (*Sylvilagus transitionalis* Bangs, 1895; Fenderson et al. 2014) but roads had no impact on the genetic structure of pygmy rabbits (Estes-Zumpf et al. 2010). Road-killed swamp rabbits were observed during the course of this study and anecdotal observations from radiotelemetry in the study area indicate swamp rabbits were reluctant to cross roads (Crawford et al. 2018). Unfortunately, we were unable to address impacts of roads at a finer scale due to the relatively limited number of swamp rabbit samples collected.

Our study provided landscape-scale information for swamp rabbits and identified canopy cover as being important for landscape connectivity of swamp rabbits on a broad geographic scale. We

457 recommend that researchers be specific in their definition of canopy cover and define their scale when
458 discussing the role of canopy cover or canopy closure in studies of swamp rabbit ecology, particularly
459 when making recommendations for forest management. Continued research into the importance of
460 mature forest versus early successional forest to swamp rabbits at multiple scales will help refine
461 recommendations for swamp rabbit habitat. Land cover alterations that do not provide canopy cover in
462 any form, such as conversion to agriculture, are highly detrimental for swamp rabbits not only by
463 removing habitat but also by replacing it with inhospitable matrix that impedes gene flow and landscape
464 connectivity. Our results support a more urgent need to conserve and restore bottomland hardwood
465 forest and conserve adjacent upland forested areas that provide canopy cover for swamp rabbits. These
466 measures are important for connecting remaining suitable habitat for swamp rabbits at the northern
467 fringe of their range thereby preventing further range contraction for this species.

468 Swamp rabbits present a challenge to conservation research, primarily due to their ephemeral
469 occupation of sites (Roy Nielsen et al. 2008), flood prone habitat (Zollner et al. 2000*b*), and relatively
470 low capture rates (0.7 individuals/100 trap nights; Scharine et al. 2011). Due to these difficulties and the
471 potential weaknesses in available landscape genetic analyses, we recommend that researchers revisit and
472 retest the conclusions from this study and other swamp rabbit research, building upon the knowledge
473 gained and hypotheses suggested by earlier work. Landscape genetics as a discipline has received
474 considerable methodological criticism and re-evaluation (e.g., Legendre and Fortin 2010; Segelbacher et
475 al, 2010; Storfer et al. 2010; Guillot and Rousset 2012; Graves et al. 2013; Wagner and Fortin 2013)
476 despite the persistent need for the information such studies provide in the face of biodiversity loss from
477 habitat fragmentation (Manel and Holderegger 2013). We demonstrated that concordance of multiple
478 landscape genetics methods can be achieved with empirical genetic data and landscape genetic studies
479 can provide critical landscape-scale information, even when species are cryptic and difficult to study.

We recommend that the uncertainties that remain regarding some of the core methods such as Mantel tests should not discourage researchers from attempting landscape genetics studies which can yield insight for imperiled and specialist species that may otherwise be impossible to obtain through other methods.

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Supplementary Material

Supplemental Fig. S1

Supplemental Table S2

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Table 1. Resistance values for the landscape attributes derived from expert opinion models (Robinson et al. 2016).

Model	expert weight	exponential expert weight
Land cover		
Open water, barren, developed	27	729
Agriculture	18	324
Grassland	11	121
Upland forest	9	81
Wetland emergent	3	9
Wetland forest	2	4
Canopy		
0-25%	19	361
26-50%	9	81
51-75%	6	36
76-100%	5	25
Roads		
Highways	18	324
Secondary	10	100
Local/Rural	6	36
Unpaved	6	36

Note: Values were incorporated into a series of resistance surfaces (expert weight and exponential expert weight) used to examine the relationship between landscape resistance and genetic distance of individual swamp rabbits (*Sylvilagus aquaticus*) sampled from southern Illinois from 2004-2011.

782 Table 2. Values (binary/binary exponential) for resistance surfaces (wetland, upland, disturbed, high
783 canopy, highway, large road) used to examine the relationship between landscape resistance and genetic
784 distance of individual swamp rabbits (*Sylvilagus aquaticus*).
785

Attribute	wetland	upland	disturbed	high canopy	highway	large road*
Land Cover						
Open water, barren, developed	10/100	1	10/100			
Agriculture	10/100	1	10/100			
Grassland	10/100	10/100	1			
Upland forest	10/100	10/100	1			
Wetland emergent	1	1	1			
Wetland forest	1	1	1			
Canopy						
0-25%				10/100		
26-50%				10/100		
51-75%				1		
76-100%				1		
Roads						
Highways					10/100	10/100
Secondary					1	10/100
Local/Rural					1	1
Unpaved					1	1

786
787 *Includes highways and secondary roads

Table 3. Results of the first step of causal modeling (Wasserman et al. 2010) testing candidate surfaces (R: roads, L: land cover, C: tree canopy cover, and W: watercourses) of landscape resistance versus individual genetic distance for swamp rabbits (*Sylvilagus aquaticus*).

Model	Simple G~L		Partial G~L Eq		Partial G~Eq L		RS
	Mantel <i>r</i>	<i>P</i>	Mantel <i>r</i>	<i>P</i>	Mantel <i>r</i>	<i>P</i>	
L + C	0.2918	< 0.001	0.2184	< 0.001	-0.0500	0.857	0.2684
R + C	0.2917	< 0.001	0.2136	< 0.001	-0.0199	0.666	0.2334
C	0.2917	< 0.001	0.2133	< 0.001	-0.0167	0.639	0.2300
L + R + C	0.2916	< 0.001	0.2184	< 0.001	-0.0513	0.870	0.2697
C + W	0.2913	< 0.001	0.2140	< 0.001	-0.0288	0.731	0.2428
R + C + W	0.2912	< 0.001	0.2143	< 0.001	-0.0315	0.751	0.2458
L + C + W	0.2910	< 0.001	0.2186	< 0.001	-0.0559	0.881	0.2745
L + R + C + W	0.2908	< 0.001	0.2186	< 0.001	-0.0570	0.891	0.2756
L + R + W	0.2685	< 0.001	0.1781	< 0.001	-0.0032	0.528	0.1813
L + W	0.2684	< 0.001	0.1779	< 0.001	0.0006	0.502	0.1773
L + R	0.2667	< 0.001	0.1760	< 0.001	0.0174	0.348	0.1586
L	0.2661	< 0.001	0.1757	< 0.001	0.0235	0.303	0.1522
R	0.2193	< 0.001	0.0924	0.043	0.0235	0.296	0.0688
R + W	0.2171	< 0.001	0.1123	0.010	-0.0836	0.960	0.1958
W	0.2137	< 0.001	0.0809	0.048	-0.0491	0.842	0.1300

Note: Three Mantel tests were performed for the first step of causal modeling: (1) G, genetic distance, regressed against L, the candidate model (G~L); (2) genetic distance versus the candidate model with Eq, an equal cost model, as the confounding factor (G~L|Eq); and (3) genetic versus the equal cost model with the candidate model as the confounding factor (G~Eq|L). Models were regarded as supported if the first and second tests produced a significant result and the third produced a non-significant result. The difference between the Mantel *r* from the two partial tests is called the relative support (RS).

Table 4. Results of the second step of causal modeling (Wasserman et al. 2010) testing landscape resistance surfaces (R: roads, L: land cover, C: tree canopy cover, and W: watercourses) with individual genetic distance for swamp rabbits (*Sylvilagus aquaticus*).

Alternate model	G~T A		G~A T	
	Mantel <i>r</i>	<i>P</i>	Mantel <i>r</i>	<i>P</i>
R + C	0.0394	0.217	0.0384	0.225
C	0.0404	0.202	0.0393	0.222
L + R + C	0.0482	0.147	-0.0468	0.846
C + W	0.0390	0.210	0.0349	0.248
R + C + W	0.0387	0.215	0.0338	0.255
L + C + W	0.0471	0.158	-0.0412	0.808
L + R + C + W	0.0495	0.145	-0.0424	0.815
L + R + W	0.1268	0.005	-0.0453	0.814
L + W	0.1263	0.005	-0.0432	0.809
L + R	0.1279	0.004	-0.0361	0.769
L	0.1285	0.003	-0.0329	0.746
R	0.2019	< 0.001	-0.0438	0.816
R + W	0.2025	< 0.001	-0.0346	0.759
W	0.2051	< 0.001	-0.0274	0.717

Note: The top model (T) found in the first step, dispersal habitat with barrier, was related in a partial Mantel test with other supported models (A) as the causal factor (G~T|A) and the confounding factor (G~A|T).

Table 5. Results from a redundancy analysis in which genetic distances were regressed against spatial predictors including sample coordinates and Moran Eigenvector Maps generated from least cost paths through hypothesized resistance surfaces with variables tree canopy cover (C), land cover (L), roads (R), and watercourses (W).

	all R^2	P	model R^2	P	coordinate R^2	P
C + W	0.3133	0.001	0.2144	0.001	0.0061	0.277
R + C	0.3119	0.001	0.2130	0.001	0.0038	0.362
Euclidean	0.3090	0.001	0.2101	0.001	0.0411	0.002
C	0.3064	0.001	0.2076	0.001	0.0051	0.299
L + R + C + W	0.2999	0.001	0.2011	0.001	0.0877	0.001
R + W	0.2857	0.001	0.1868	0.001	0.0006	0.489
R + C + W	0.2843	0.001	0.1854	0.001	-0.0104	0.810
W	0.2649	0.001	0.1660	0.001	0.0013	0.411
R	0.2586	0.001	0.1597	0.001	-0.0009	0.506
L + C + W	0.2346	0.001	0.1357	0.001	0.0804	0.001
L + C	0.2317	0.001	0.1328	0.001	0.0793	0.001
L + R + C	0.2315	0.001	0.1326	0.001	0.0809	0.001
equal cost	0.2299	0.001	0.1310	0.001	-0.0177	0.927
L + R	0.1448	0.001	0.0459	0.006	0.0661	0.001
L + W	0.1416	0.001	0.0427	0.005	0.0870	0.001
L + R + W	0.1350	0.001	0.0361	0.001	0.0695	0.001
L	0.0865	0.001	-0.0124	0.964	0.0543	0.004

Note: Variation was partitioned among all spatial predictors (all), the least cost paths (model), and the coordinates. Significance was determined with 999 iterations. Euclidean distance (Euclidean) was included as a null model.

Figure 1. Swamp rabbit (*Sylvilagus aquaticus*) sample locations (diamonds) for a landscape genetics analysis in southern Illinois, USA. The top left inset depicts the state of Illinois and the study area (black box) in relation to the eastern half of the USA. The numbers of individual genotypes are shown adjacent to locations and the designation “P” indicates that the genotype originated from a fecal pellet. All other genotypes were obtained from tissue samples. Dark grey lines represent interstate highways (I57 and I24) and light grey lines represent watercourses. Major watercourses and states are labeled.

Figure 2. Mantel correlations and 95% confidence intervals (error bars) for the relationship between a suite of resistance surfaces and genetic distance of swamp rabbits (*Sylvilagus aquaticus*) from southern Illinois, USA. Mantel correlations were compared among surfaces representing land cover (lc), canopy, roads, and watercourse corridors of two widths (60 m, 800 m) and a watercourse corridor considering only 2nd order and higher streams (800 m 2nd order). Resistance values were derived from expert opinions of the impact of each attribute (expert) and binary surfaces (disturbed, wetland, upland, high canopy, large road, highway) in which two values were assigned, one for the attribute and one for the background. Exponential transformations of the resistance values (exp) were also considered.

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Figure 1. Swamp rabbit (*Sylvilagus aquaticus*) sample locations (diamonds) for a landscape genetics analysis in southern Illinois, USA. The top left inset depicts the state of Illinois and the study area (black box) in relation to the eastern half of the USA. The numbers of individual genotypes are shown adjacent to locations and the designation "P" indicates that the genotype originated from a fecal pellet. All other genotypes were obtained from tissue samples. Dark grey lines represent interstate highways (I57 and I24) and light grey lines represent watercourses. Major watercourses and states are labeled.

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