

# Circuit theory to estimate natal dispersal routes and functional landscape connectivity for an endangered small mammal

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## Abstract

**Context** Natal dispersal links population dynamics to landscape connectivity. Understanding how organisms perceive barriers to movement, or landscape resistance, during natal dispersal is important to conserve and manage populations threatened by fragmentation and habitat loss.

**Objectives** We aimed to (1) model probability of landscape use by an endangered small mammal (*Tamiasciurus hudsonicus grahamensis*) in the Pinaleno Mountains, Arizona, USA as a function of forest structure at the population and intra-population level, (2) identify potential natal dispersal pathways between natal and settlement locations based on landscape resistance scenarios, and (3) assess which resistance surface best represented observed exploration, dispersal, and settlement.

**Methods** We modeled probability of habitat use via used and available animal locations. We developed three landscape resistance scenarios to represent individual differences in perceived resistance. We

used circuit theory to identify potential long-distance dispersal pathways and to assess which resistance scenario best represented observed forest use and settlement.

**Results** Top probability of forest use models included physical landscape features, forest structure, and burn severity. Composite connectivity models, created from multiple resistance scenarios, identified areas that may promote long distance dispersal movements. Connectivity models developed from only natal focal nodes allowed for assessment of resistance scenarios; a non-linear, negative-exponential relationship between probability of use and resistance best represented observed exploration and settlement.

**Conclusions** Circuit theory is a useful tool to identify potential small mammal movement pathways when high temporal resolution movement data are limited, and for assessing how well resistance scenarios represent observed settlement patterns.

**Keywords** Arizona · Circuitscape · Pinaleno Mountains · Point selection function · Resistance surface · Small mammal

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## Introduction

Many wildlife species face a world that is increasingly impermeable to movement as a result of habitat fragmentation and degradation, with limited

connectivity among habitat patches (Theobald et al. 2012). Conservation of landscape connectivity is therefore essential to sustain wildlife populations, support animal movements, and maintain gene flow (Lindenmayer and Fischer 2006; Wade et al. 2015), and is of increasing concern as species' ranges or critical habitats are predicted to shift under global climate change scenarios (Carroll et al. 2010; Zeller et al. 2012; Lawler et al. 2013). Landscape connectivity comprises two parts: structural connectivity, the physical features that link habitat patches, and functional connectivity, which is species- and context-specific and reflects how well individuals within a population can access locations based upon their internal state and motivation (Betts et al. 2015). Consideration of both components is necessary to model and assess connectivity, particularly in species of conservation concern.

Natal dispersal, the unidirectional permanent movement of young animals from the natal area to a new territory or home range (Greenwood 1980), is a key process that links population dynamics and landscape connectivity. Although natal dispersal occurs only once for an individual, these movements are context-specific and often represent the greatest distance that an individual moves in their lifetime. Quantification of such movements is therefore critical to understand movement capacity of a species as well as providing a way to assess functional landscape connectivity. Despite the importance for critical habitat designation, characterization of metapopulation dynamics, parameterization of species distribution models, population viability assessment, and potential range shift projections, natal dispersal remains poorly understood (Delgado et al. 2010). However, recent advances in telemetry technology include wearable VHF (very high frequency) transmitters and GPS (global positioning system) tags that continue to become ever more miniaturized and allow for increased spatial accuracy and temporal frequency of animal location estimates (Kie et al. 2010). Such capabilities provide a more complete representation of animal movement, from which we can infer resource selection, analyze movement paths, and fully capture natal dispersal and the magnitude of dispersal movements.

Small animals (<300 g) comprise 81 and 67% of the world's bird and mammal fauna respectively (Wikelski et al. 2007), and pose a particular challenge

for the study of natal dispersal. Due to their small body size, tracking options for small animals have been constrained to VHF transmitters with shorter ranges (Wikelski et al. 2007; Lookingbill et al. 2010). Thus, we are often presented with an incomplete picture of dispersal in many small species. Yet understanding natal dispersal and associated long-distance movements in small animals is necessary to fully characterize functional landscape connectivity, as small animals tend to perceive landscape fragmentation at finer scales (Gehring and Swihart 2003; McDonald and St. Clair 2004), and small barriers can impede dispersal movements for some species (Fischer and Lindenmayer 2007). For example, relatively small habitat gaps <100 m and roads <20 m are often beyond the perceptual range of many small mammals (Mech and Zollner 2002; Forero-Medina and Vieira 2009; Bridgman et al. 2012; Chen and Koprowski 2016). Within a species, perceptual abilities are context dependent, and can be affected by environmental factors such as wind or humidity, matrix composition, visual obstruction, and life history (Forero-Medina and Vieira 2009). Further, individuals may perceive landscape resistance, and move through the landscape differently, depending upon physical condition, behavioral state, and biotic and structural composition of the natal area (Bakker and Van Vuren 2004; Stamps 2006; del Mar Delgado and Penteriani 2008; Mabry and Stamps 2008; Clobert et al. 2009; Delgado et al. 2010; Zeller et al. 2014). Thus, external conditions and individual traits can influence functional connectivity and lead to different dispersal outcomes within a population.

Documentation of natal dispersal movements, landscape use during dispersal, and identification of high connectivity areas is especially important for threatened and endangered species as it ensures that conservation efforts effectively target important corridors connecting habitat patches as well as the identification of areas currently limiting connectivity. We often lack key data on movement and dispersal capabilities of endangered species (Lookingbill et al. 2010), and must estimate likely movements based upon our knowledge of species' associations with ecological variables, and condition-dependent factors that can influence an individual's motivation to move.

Electric circuit theory can be used to link landscape composition and pattern to functional connectivity by intuitively transforming landscapes and an animals'

potential to move within them into current, voltage, and resistance values, concepts that are directly relatable to random-walk movement theory (McRae et al. 2008). Circuit theory is a tool to test hypotheses related to landscape connectivity, how landscape features promote or impede movement, and their implications for dispersal and gene flow in wildlife populations at local (St-Louis et al. 2014) and landscape spatial scales (McRae and Beier 2007; McRae et al. 2008; Wade et al. 2015). In circuit theory-based models, current flowing between any pair of nodes is equivalent to the number of times a simulated individual moves along that path (McRae et al. 2008). High current density between nodes identifies pathways potentially important for landscape connectivity (McRae et al. 2008). Because circuit theory operates within a resistance surface, a user-defined geospatial layer where resistance to movement is represented as a numeric score in each grid cell, it is ideal for incorporating variability in perceived landscape resistance among individuals. While least cost connectivity models are commonly employed to identify likely corridors or dispersal pathways (e.g. Stevenson-Holt et al. 2014; Wade et al. 2015), they often identify one least cost path or summarize across top least cost paths, whereas circuit theory-based methods allow for the identification of multiple movement paths (McRae et al. 2008). In the absence of sufficient movement data obtained during natal dispersal, circuit theory can be applied post hoc to identify potential dispersal corridors, or routes that secretive animals may have taken based upon habitat use (e.g. Lookingbill et al. 2010; St-Louis et al. 2014).

Here we use circuit theory to model the demographic functional connectivity (*sensu* Wade et al. 2015) of a mixed conifer forest from the perspective of a federally endangered small mammal. We address the following research questions (1) what are likely movement paths juveniles take during long distance dispersal, and (2) which resistance surface best reflects observed exploration, dispersal, and settlement? We use known animal locations obtained primarily before and after natal dispersal within a point selection function (a resource selection function based on points, or animal locations) to estimate probability of use of a forested landscape. We identify areas that appear to promote the movement and recruitment of juveniles into new settlement locations following long distance dispersal events based upon three resistance

scenarios that account for individual heterogeneity in perceived landscape resistance. We then compare our three increasingly restrictive resistance scenarios to determine which best represents functional landscape permeability and promotes observed exploration, dispersal, and settlement movements.

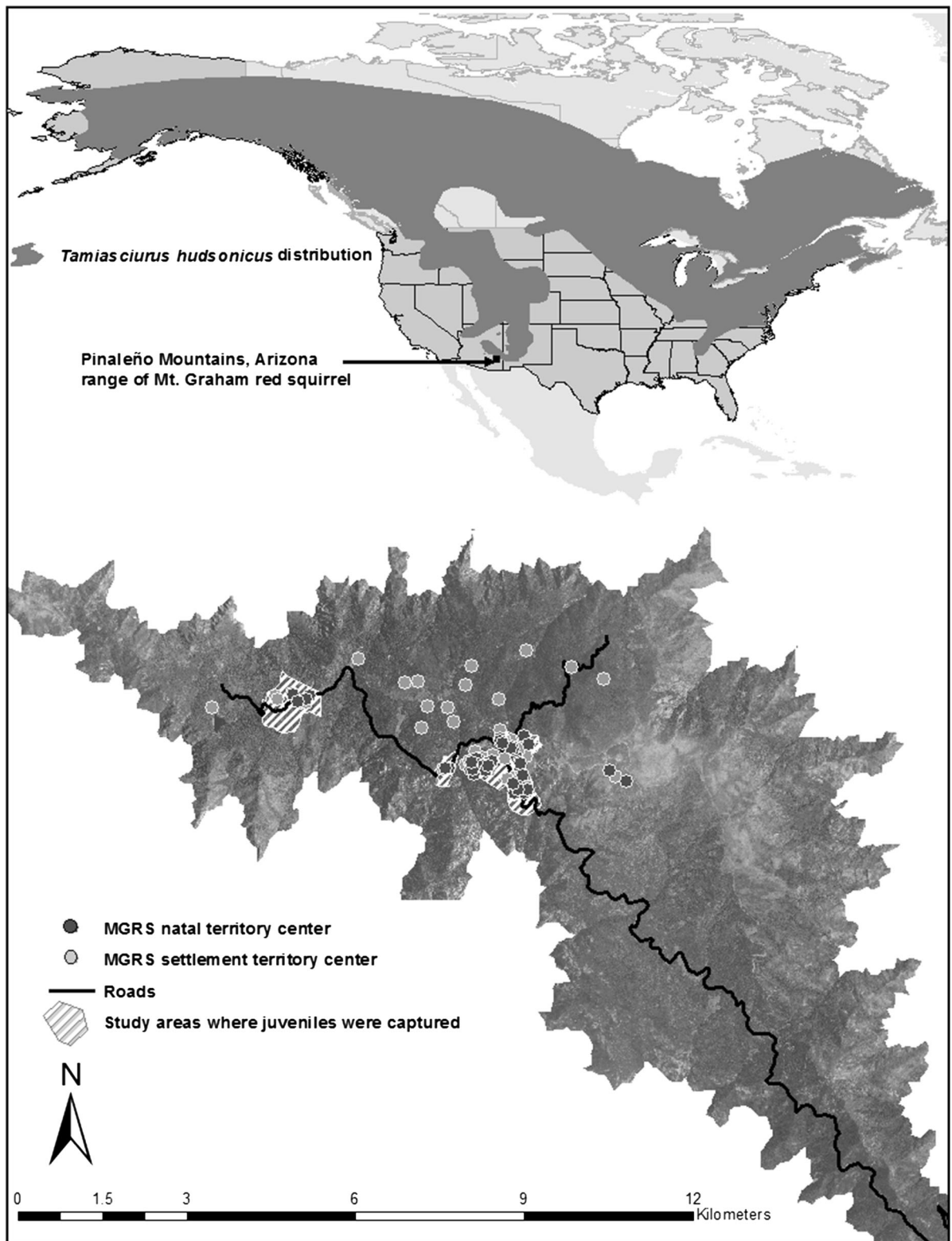
## Methods

### Study organism

The Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*; hereafter MGRS) is an endangered subspecies of North American red squirrel restricted to mature spruce-fir and mixed-conifer forest in the Pinaleño Mountains, in southeastern Arizona, USA, 32.7017°N, 109.8714°W. The Pinaleño Mountains are part a series of high-elevation peaks rising from desert grassland, known as the Madrean Archipelago. These mountain ranges are hot spots of biodiversity (Spector 2002), and also of conservation concern as the distributions of many less vagile species are constrained. MGRS represents the southernmost population of red squirrels in North America (Sanderson and Koprowski 2009; Fig. 1), and it is estimated that MGRS have been isolated for at least 10,000 years following post-Pleistocene glacial retreat (Harris 1990). MGRS are morphologically, vocally, and genetically distinct from their nearest conspecific (Koprowski et al. 2005; Fitak et al. 2013), and have recently been assigned to a new species of southwestern *Tamiasciurus* (*T. fremonti*) based upon systematics and niche-based divergences (Hope et al. 2016). Despite being a relatively small mammal (200–250 g) (Steele 1998), MGRS move substantial distances during natal dispersal, distances that are far greater than reported for other red squirrel populations (Merrick and Koprowski 2016a). Thus, maintenance of connectivity and promotion of long distance dispersal movements in the wake of recent habitat loss are conservation priorities.

### Study area

Our study areas comprised vegetation communities of mesic mixed conifer forest and high-elevation spruce fir forest in the Pinaleño Mountains in southeastern Arizona, USA (Smith and Mannan 1994; O'Connor



◀ **Fig. 1** Top Overview of the distribution of North American red squirrels (*Tamiasciurus hudsonicus*) with the Pinaleno Mountains shown in black. Bottom Mt. Graham red squirrel habitat above 2348 m in elevation and associated study areas in the Pinaleno Mountains, Arizona USA where juveniles were captured. Natal and settlement sites obtained from radio-collared juveniles shown in dark gray and light gray circles respectively

et al. 2014). MGRS habitat occurs above 2591 m, and our study areas range in elevation from 2647 to 3267 m. Fires in 1996 and 2004 burned a combined 14,160 ha of pine, mixed conifer, and spruce-fir forest (45% of the forest above 2135 m) which, combined with tree death from insects, reduced spruce and cork-bark fir area by 66% (O'Connor et al. 2014), which results in a patchy mosaic of healthy forest within a matrix of dead or dying trees (Fig. 2).

#### Animal capture and radio-telemetry

Between May 2010 and February 2014 we trapped, radio-collared, and followed 94 juvenile MGRS through dispersal, settlement, and post-settlement. Methods for capture, marking, and radio-collaring individuals are reported elsewhere (Merrick and Koprowski 2016a, b). We tracked individuals weekly from time of capture until settlement and monitored radio-collared juveniles for 4 h time blocks in which we located individuals once every hour (Merrick and Koprowski 2016a, b).

#### Ecological variables

We used discrete-return aerial LiDAR (light detection and ranging) to assess forest structure and physical landscape features important for MGRS site selection (Smith and Mannan 1994; Merrick et al. 2007). LiDAR data were acquired in September 2008 (after recent fires) within the 34,600 ha mixed-conifer and spruce-fir zones above 2133 m with a pulse-return spacing of 7.86 points/m<sup>2</sup> (Laes et al. 2009). We used 6 primary and 1 secondary LiDAR-derived variables at 25 m resolution (grid cell size) for modeling MGRS probability of use: elevation (m), aspect (Beers et al. 1966), slope (%), canopy cover (%), mean tree height (m), standard deviation in tree height (a characteristic associated with forest stand age), and a ratio of living basal area (m<sup>2</sup>) to total basal area (m<sup>2</sup>) (Laes et al. 2009; Mitchell et al. 2012). We included

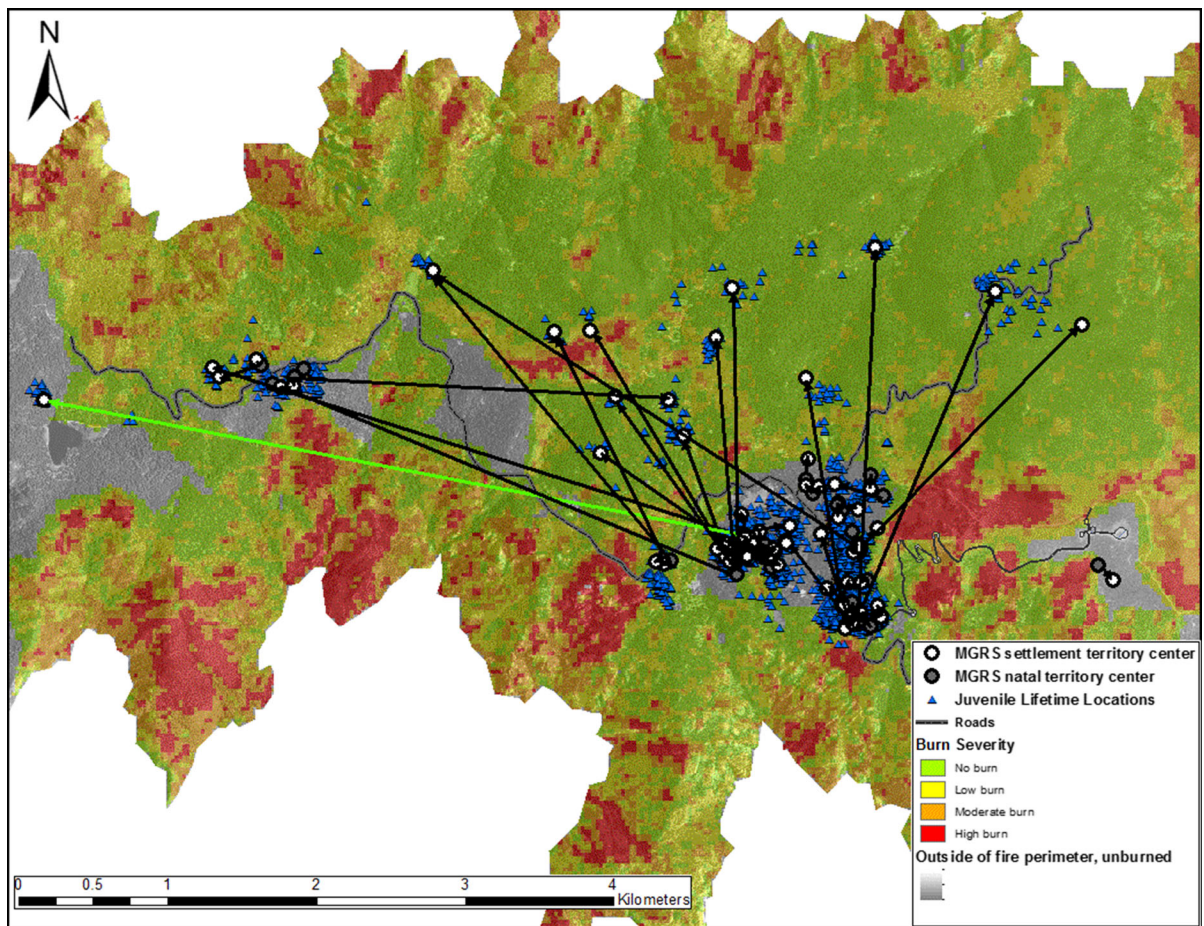
Monitoring Trends in Burn Severity (MTBS; <http://www.mtbs.gov/>) 30 m resolution Landsat-derived fire perimeter and fire severity grids for recent Clark Peak (1996) and Nuttall Complex (2004) fires, averaged in areas of burn perimeter overlap, (Fig. 2). We resampled the MTBS grids to 25 m to match the resolution of LiDAR products and masked all variables to elevations >2438 m.

Mean red squirrel territory size is 0.24–0.98 ha (Steele 1998), therefore a grid cell size of 25 m is appropriate for this species. From 2002 to 2014, mean fall home range size (dispersing MGRS settle in the fall) for MGRS was 1.7 ha—a diameter of 147 m, or the equivalent of 6, 25 m pixels; a grid cell size that adequately captures heterogeneity in forest and landscape features to which MGRS respond to during habitat selection.

#### Modeling probability of habitat use

We examined the importance of LiDAR-derived variables and burn severity on MGRS landscape use from the population and intra-population perspective. To develop our habitat use versus availability models, we calculated 70% fixed kernel home ranges via least squares cross validation (Hooze and Eichenlaub 2000) for each individual for which we had obtained ≥20 telemetry locations between 1 September 2010 and 28 February 2014 (n = 81). We used animal locations falling within the 70% fixed home range kernels (n = 10,560) to develop resource selection and probability of habitat use models and considered locations falling outside of the 70% fixed home range kernels as exploration and dispersal movements (n = 98) which we used to validate our probability of habitat use and connectivity scenarios. Within each home range kernel we generated 105 available locations such that available locations (n = 8505) were stratified by individual (Buja and Menza 2013). We developed population-level resource selection generalized linear models (GLMs) and intra-population conditional mixed-effects logistic resource selection mixed models (GLMMs) (Duchesne et al. 2010) in R package lme4 (Bates et al. 2015) with a binary response (1 = locations used by 81 MGRS radio-collared as juveniles, 0 = available locations) and binomial error structure to model probability of habitat use by juvenile MGRS. For GLMMs we included sex and litter ID as additional fixed effects and animal ID as a





**Fig. 2** Natal (gray circles) and settlement sites (white circles) for 63 individuals that successfully settled and lifetime telemetry locations (blue triangles) for 94 juvenile Mt. Graham red squirrels in the Pinaleño Mountains, Arizona USA. Black arrows indicate individual straight-line dispersal vectors relative to the extent of recent fires in 1996 and 2004. The green vector is the longest dispersal event recorded during this study

(4.9 km). Burn severity estimates obtained from USDA Forest Service Monitoring Trends in Burn Severity (MTBS) are shown with red and orange colors representing moderate to high burn, yellow and green colors represent little to no burn within the fire perimeters. Areas outside of the fire perimeters are in gray color scale and were not affected by the recent fires

random effect. We sampled the pixel value of the eight ecological variable grids at each of the 19,065 locations and modeled probability of habitat use as a point selection function where use is a function of ecological variables (Boyce et al. 2002; Manly et al. 2002; Zeller et al. 2012). We assessed multicollinearity among ecological variables by calculating the variance inflation factor (VIF) in package DAG (Maingdonald and Braun 2015). All explanatory ecological variables within a global model had low multicollinearity ( $VIF < 4.6$ ).

To understand the relative explanatory power of the physical landscape, forest structure, and burn severity

on landscape use by MGRS, we developed three model subsets for both unconditional population-level resource selection via GLM and intra-population conditional resource selection via GLMM. Within each model subset, we assessed the importance of each component variable in predicting juvenile MGRS landscape use by adding in each variable sequentially. The subsets included: 1. physical landscape (elevation, slope, and aspect;  $n = 3$  models), representing the landscape bare of biotic forest features; 2. forest structure (canopy cover, live basal area: total basal area ratio, mean tree height, and standard deviation in tree height;  $n = 4$  models); and 3. burn severity

(MTBS burn severity class;  $n = 1$  model). We compared the top models from each subset in addition to a null and global model within an information-theoretic model selection framework (Table 1). We considered models with the lowest  $AIC_c$  (Akaike information criterion corrected for small sample size) score to be the top candidate models and considered models within  $\Delta AIC_c \leq 2$  from the top model as competing. Each model subset and their associated rankings serve to aid in understanding the relative importance of the physical landscape, forest structure, and burn severity in determining population-level and intra-population resource selection. We calculated model-averaged coefficients from a model set that consisted of a global model, and component models of each subset in package `AICcmodavg` (Mazerolle 2015) (Table 2).

We applied our model-averaged coefficients from the (global) intra-population conditional GLMM ( $\beta$ ; Table 2) within a resource selection function (Manly et al. 2002) in ArcGIS 10.3 to generate a probability of use grid with 25 m cell size (Fig. 3). Here we assume that squirrels make decisions about where to move on the landscape based upon preferences similar to those for selecting habitat (Zeller et al. 2012).

### Modeling landscape resistance

Estimation of how landscape features are perceived by organisms and influence their willingness to move through a matrix is difficult, yet characterization of landscape resistance is among the most important steps in connectivity analyses as results are sensitive to the underlying resistance surface (Gonzales and Gergel 2007; Trainor et al. 2013; Stevenson-Holt et al. 2014; Zeller et al. 2014; Wade et al. 2015). Animals may perceive and respond to landscape features differently depending on their experience in the natal area, internal physiological state, and behavioral phenotype (Bowler and Benton 2005; Stamps 2006; Clobert et al. 2009). We developed three landscape resistance scenarios that varied the relationship between probability of use and landscape resistance to represent individual heterogeneity in perceptions of functional landscape permeability. We used Eq. 1 from Trainor et al. (2013) to calculate 1 linear and 2 non-linear resistance or friction surfaces ( $f$ ) where  $h$  is the probability of use value of each grid cell obtained from the above resource selection function, and  $c$  is a rescaling parameter determining

the shape of the curve relating probability of use and resistance to movement (Eq. 1).

$$f = 100 - 99 \frac{1 - \exp(-ch)}{1 - \exp(-c)} \quad (1)$$

For the scaling parameter ( $c$ ), we used values = 0.25, 2, and 16, where  $c = 0.25$  approaches a linear function ( $f = 1 - h$ ) and is our most prohibitive resistance surface,  $c = 16$  approaches a negative exponential ( $f = h^{-1}$ ) and is our least prohibitive resistance surface, and  $c = 2$  produces in an intermediate, non-linear resistance surface (Fig. 3). Resistance surfaces varied from values of 5.16–92.54, where cells with a value approaching 100 represent the highest resistance to movement. We conducted two separate connectivity analyses based upon each of the three resistance surfaces.

### Circuit theory to model possible long distance dispersal pathways

We used Circuitscape 4.0 (McRae et al. 2009) to estimate functional connectivity in two ways: first to identify potential dispersal corridors between natal and settlement sites within a patchy forest mosaic, and second to assess which resistance surface resulted in the highest electrical current at settlement, exploration, and dispersal locations.

To identify highly connected regions between natal and settlement sites, we generated mean current density surfaces based upon 1:1 iterations between independent source nodes (natal grid cells) and ground nodes (cells in which juveniles settled) in advanced modeling mode with raster data. For each run, we specified that sources and grounds be activated independently and set all source nodes to have a unit current value of 1, and all ground nodes to have a value of zero. We ran this model for each resistance surface, and specified log-transform current maps as the desired output (Fig. 4).

To assess which resistance surface best represented functional landscape permeability for dispersing MGRS, we generated current density surfaces in pairwise mode with raster data and specified a one to many relationship among a set of source nodes (natal grid cells only). In this configuration, current flow is estimated across the landscape from each source to all other sources. We ran this model for each resistance surface and specified log-transform current maps as

**Table 1** Multi-model selection results based upon Akaike Information criterion corrected for small sample size (AICc) and log likelihoods (LL) for 3 model subsets (physical landscape, forest structure, burn severity) within population-

level generalized linear models (GLMs; top panel) and intra-population level generalized linear conditional mixed models (GLMM; bottom panel)

	K	AICc	Delta AICc	AICc wt	Cum. wt	LL
<i>Population-level unconditional models</i>						
Subset 1: physical landscape variables						
Elevation + slope + aspect	4	26,043.55	0	0.93	0.93	-13,017.77
Elevation + aspect	3	26,048.72	5.18	0.07	1	-13,021.36
Elevation	2	26,071.92	28.38	0	1	-13,033.96
Subset 2: forest structure variables						
Balv. ratio, cc, avght, stdvht	5	25,802.47	0	1	1	-12,896.23
Balv. ratio, cc, avght	4	26,030.24	227.78	0	1	-13,011.12
Balv. ratio, cc	3	26,085.92	283.45	0	1	-13,039.96
Balv. ratio	2	26,106.82	304.36	0	1	-13,051.41
Subset 3: burn severity						
Max burn	2	25,701.18	NA	NA	NA	NA
Model set ranking (top in each subset)						
Global (physical landscape + forest structure + burn severity)	9	25,384.56	0	1	1	-12,683.27
Subset 3: burn severity (maxburn)	2	25,701.18	316.62	0	1	-12,848.59
Subset 1: physical landscape (elevation + slope + aspect)	4	25,802.47	417.91	0	1	-12,896.23
Subset 2: forest structure (balv. ratio + cc + avght + sdvht)	5	26,043.55	658.99	0	1	-13,017.77
Null (intercept)	1	26,209.76	825.21	0	1	-13,103.88
<i>Intra-population conditional models</i>						
Subset 1: physical landscape variables						
Elevation	5	22,450.4	0	0.54	0.54	-11,220.2
Elevation + aspect	6	22,451.66	1.26	0.29	0.82	-11,219.83
Elevation + slope + aspect	7	22,452.64	2.25	0.18	1	-11,219.32
Subset 2: forest structure variables						
Balv. ratio, cc, avght, stdvht	8	22,223.43	0	1	1	-11,103.71
Balv. ratio, cc, avght	7	22,270.39	46.96	0	1	-11,128.19
Balv. ratio, cc	6	22,281.25	57.82	0	1	-11,134.62
Balv. ratio	5	22,378.84	155.41	0	1	-11,184.42
Subset 3: burn severity						
Max burn	2	22,345.23	NA	NA	NA	NA
Model set ranking (top in each subset)						
Global (physical landscape + forest structure + burn severity)	12	22,168.19	0	1	1	-11,072.09
Subset 2: forest structure (balv. ratio + cc + avght + sdvht)	8	22,223.43	55.24	0	1	-11,103.71
Subset 3: burn severity (maxburn)	5	22,345.23	177.04	0	1	-11,167.62
Null (sex + litter ID)	4	22,448.63	280.43	0	1	-11,220.31
Subset 1: physical landscape (elevation)	5	22,450.4	282.20	0	1	-11,220.2

Model sets are used identify important landscape features in predicting probability of juvenile Mt. Graham red squirrel use of forest in the Pinaleno Mountains, Arizona, USA

the desired output (Fig. 5). If current, flowing across the landscape (defined by our three resistance surfaces) among all possible natal source nodes is

relatively high at sites where animals actually settled or used during exploration and long-distance dispersal, then the resistance scenarios we developed may



**Table 2** Summary of model coefficients for fixed effects in the top (global model) predicting Mt. Graham red squirrel use of forest in the Pinaleno Mountains, Arizona, USA via

population-level generalized linear models (GLMs; top panel) and intra-population level generalized linear conditional mixed models (GLMM; bottom panel)

Global (top model) coefficients	Coefficient	Odds ratio	Lower CI	Upper CI	<i>p</i> value
Fixed effects: unconditional GLMs					
Elevation (m)	0.004	1.004	0.003	0.004	<0.000
Aspect (beers aspect)	0.060	1.062	0.015	0.105	0.009
Slope (percent slope)	-0.002	0.998	-0.007	0.004	0.597
Balv. ratio (estimated ratio living basal area:total basal area m <sup>2</sup> /ha)	0.021	1.021	0.016	0.025	<0.000
cc (percent canopy cover)	-0.005	0.995	-0.010	0.000	0.044
avght (mean tree height in m)	0.022	1.022	0.002	0.042	0.034
stdvht (standard deviation in tree height)	0.247	1.280	0.202	0.292	<0.000
maxburn (MTBS burn severity classes:0–4)	-0.415	0.660	-0.471	-0.359	<0.000
Sex (female as reference)	-	-	-	-	-
Litter ID	-	-	-	-	-
Fixed effects: conditional GLMMs					
Elevation (m)	0.002	1.002	0.000	0.003	0.020
Aspect (beers aspect)	-0.044	0.957	-0.108	0.020	0.175
Slope (percent slope)	-0.001	0.999	-0.009	0.006	0.701
Balv. ratio (estimated ratio living basal area:total basal area m <sup>2</sup> /ha)	0.007	1.007	0.000	0.012	0.024
cc (percent canopy cover)	0.009	1.009	0.003	0.015	0.002
avght (mean tree height in m)	0.009	1.009	-0.016	0.034	0.470
stdvht (standard deviation in tree height)	0.182	1.199	0.126	0.238	<0.000
maxburn (MTBS burn severity classes:0–4)	-0.314	0.730	-0.401	-0.228	<0.000
Sex (female as reference)	-0.555	0.574	-0.461	0.350	0.788
Litter ID	0.000	1.000	-0.004	0.004	0.880

adequately represent perceived landscape permeability for dispersers. We extracted the values of our one to many current flow models at each of the 98 dispersal and exploration locations and 63 settlement locations to assess model performance.

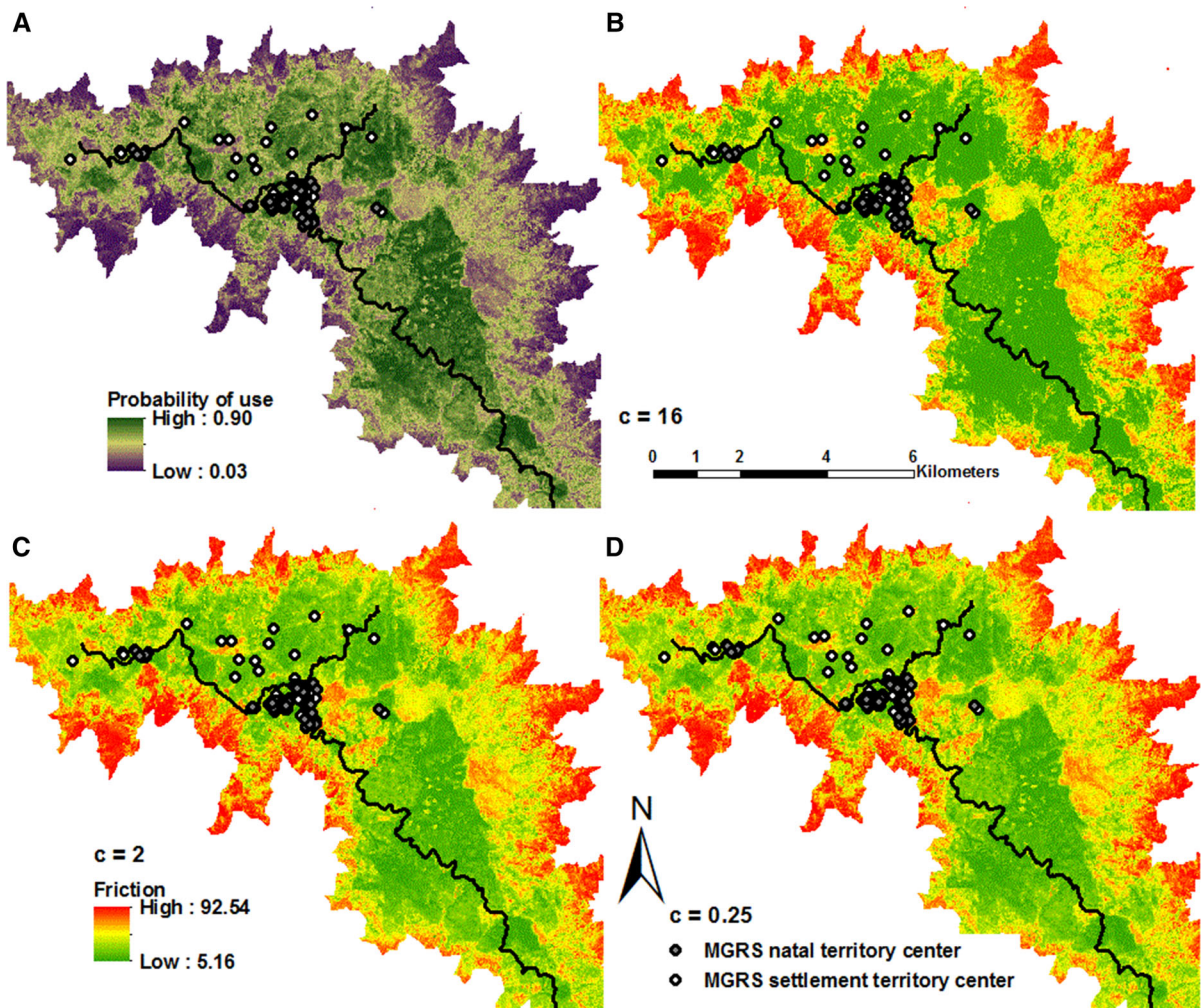
## Results

### Space use and natal dispersal

We successfully tracked 63 MGRS to settlement locations (29 females, 34 males; Fig. 2) and the maximum observed dispersal distance was 4.9 km. Although we followed focal animals regularly during the dispersal period across 4 years, we obtained few sightings ( $n = 98$ ) of MGRS during exploration and long distance dispersal movements to empirically validate estimates of connectivity.

Ecological variables important for movement decisions

Locations used by juvenile MGRS differed slightly (supplementary materials S1) in burn severity, physical topography, and forest structure from locations available to individuals in their home ranges. For both population-level GLMs and intra-population GLMMs, global models that included all three components (physical landscape, forest structure, burn severity) of mixed conifer forest received the most support. For population-level models, the second most supported model subset was burn severity, followed by physical landscape, and forest structure (Table 1). When inter-individual heterogeneity was accounted for via GLMMs, forest structure was the second most supported model subset, followed by burn severity. Each subset of ecological variables and their associated rankings can be thought of as increasingly



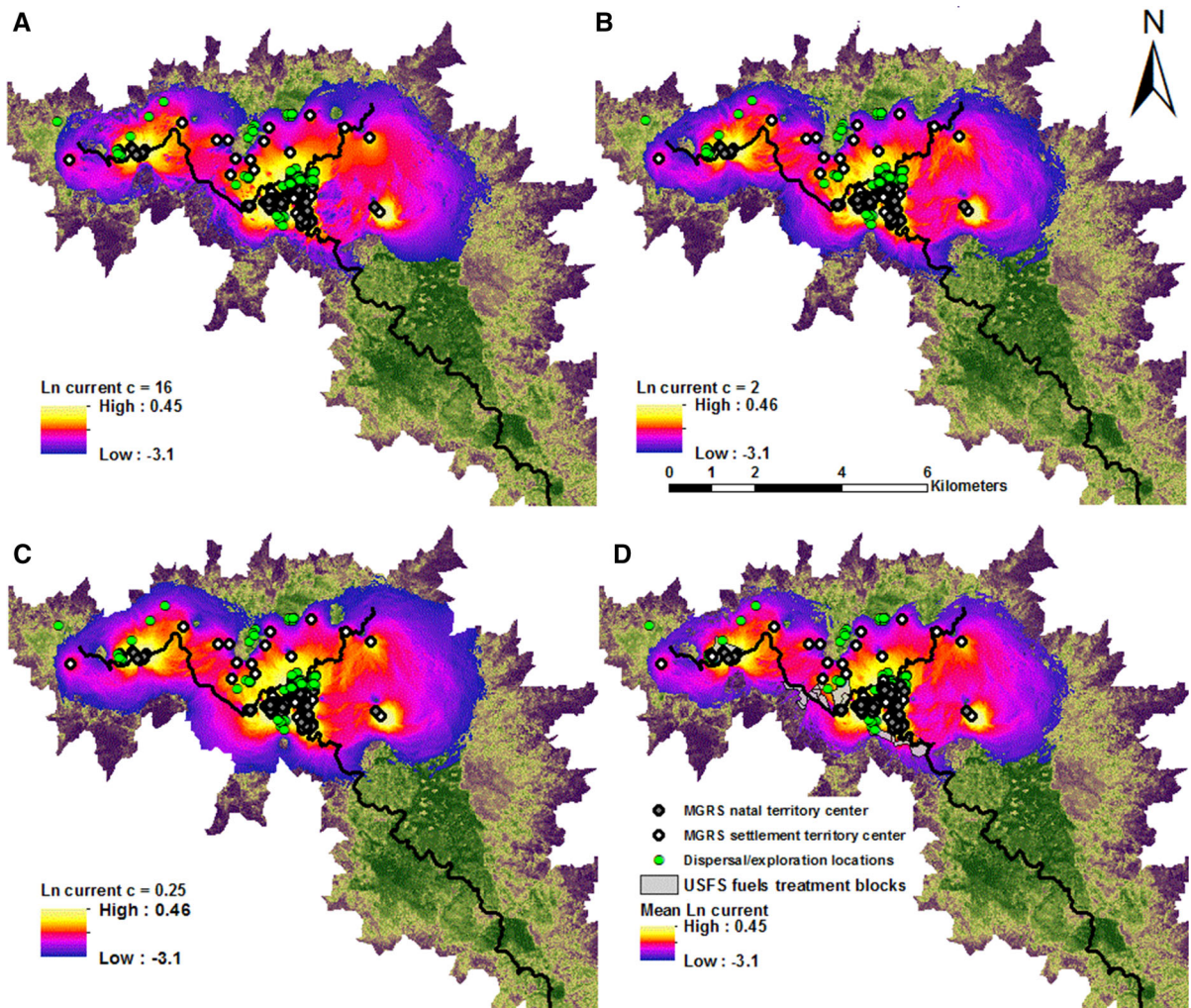
**Fig. 3** Probability of use and landscape resistance surfaces for juvenile Mt. Graham red squirrels in the Pinaleno Mountains, Arizona USA. The probability of use surface (**a**) is based on use/availability as a function of 8 ecological variables within a conditional GLMM, where high values represent forest most likely used by juvenile Mt. Graham red squirrels. Resistance

surfaces to account for individual perceptions of landscape resistance include very non-linear ( $c = 16$ ; **b**), intermediate ( $c = 2$ ; **c**), and approximately linear ( $c = 0.25$ ; **d**) transformations of the probability of use surface. High values represent areas of high resistance or friction; low values represent areas with low resistance to movement

restrictive ecological filters that determine MGRS use of a particular location. Across all individuals at the population level, locations that animals used are constrained by physical landscape features and past fire. MGRS appear to avoid areas where burn severity is equal to or exceeds moderate levels and physical topography (slope, aspect, elevation) determines where mature forest patches are likely to remain. Finally, within those forest patches, animals select for higher canopy cover, living basal area, and most importantly, mature stands of mixed age classes (mean

tree height, standard deviation in tree height; Table 1). When inter-individual heterogeneity was considered, forest structure and burn severity became more important in determining landscape features individual MGRS used within their home range (Table 1). Coefficients for top models in each subset are summarized in supplementary materials S2. Mean probability of use (based upon the conditional mixed effects resource selection global model) at 98 long distance dispersal and exploration telemetry fixes was  $0.53 \pm 0.09$  SD (range 0.31–0.69).





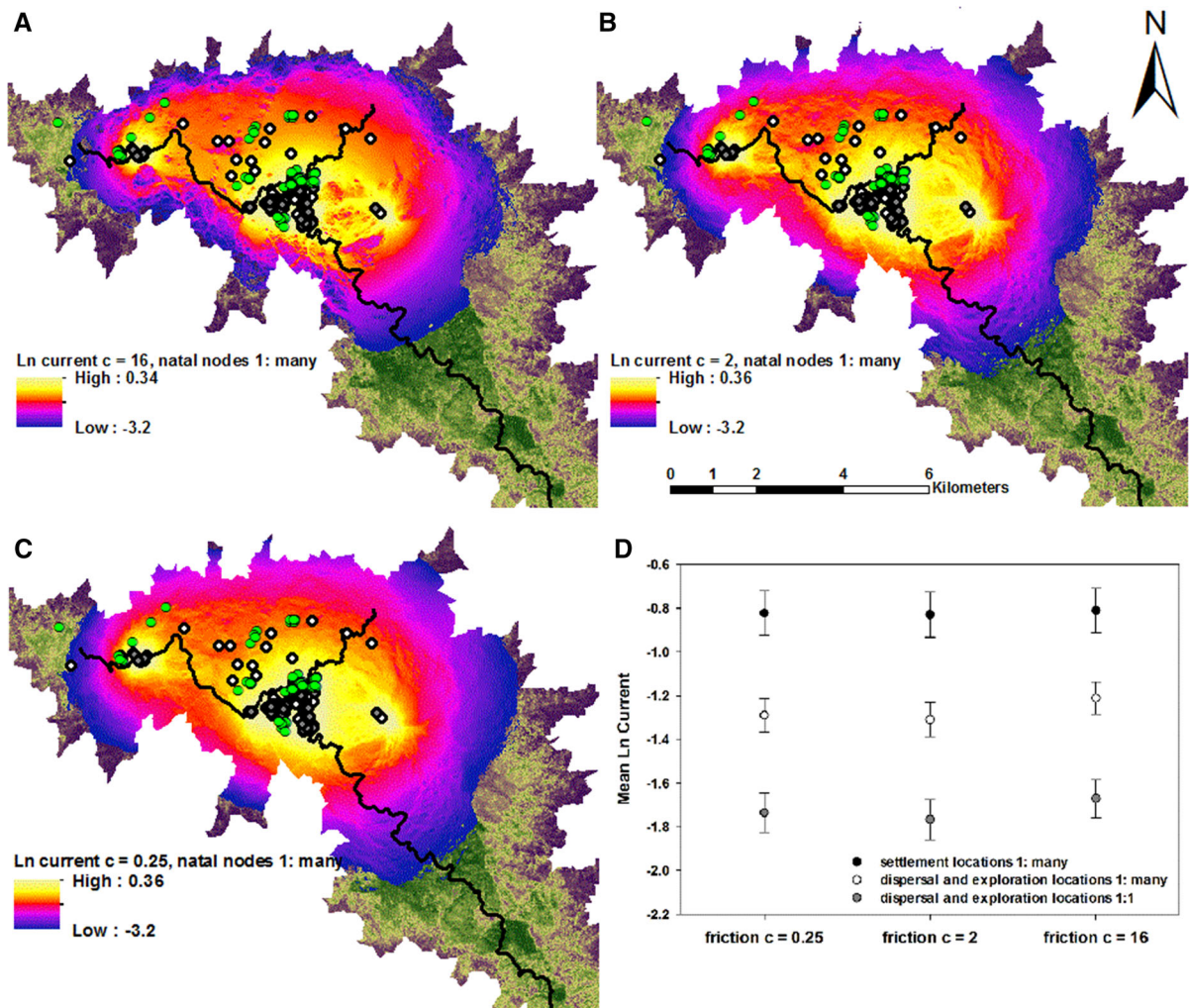
**Fig. 4** Current flow (Ln current) estimates based upon 1:1 comparisons between natal (source) and settlement (ground) nodes as a function of three increasingly prohibitive resistance functions: very non-linear ( $c = 16$ ; **a**), intermediate ( $c = 2$ ; **b**), and approximately linear ( $c = 0.25$ ; **c**) for juvenile Mt. Graham red squirrel dispersal in the Pinaleno Mountains, Arizona USA. Current densities indicate the probability of a random-walking

animal using a given cell as it passes through the landscape between source and ground nodes. Highest current densities (*warmer colors*) indicate the most likely pathways between natal and settlement sites. Panel **d** is the mean current density from the three scenarios with U.S. Forest service fuels reduction treatment blocks indicated in *gray*

### Resistance and connectivity scenarios

Our assessments of functional landscape connectivity via simulated electrical current (Figs. 4, 5) across three resistance scenarios (Fig. 3) identify areas of highest connectivity while also accounting for heterogeneity in individuals' motivation to move through and access landscape features during exploration and natal dispersal. Our most non-linear resistance surface ( $c = 16$ ) transforms all probability of use values

$\geq 0.25$  to resistance values near zero and may realistically represent landscape permeability perceived by most juveniles with sufficient stores of body fat and in a dispersal-prone behavioral state, recognizing that even marginal habitat may support rapid dispersal movements among forest patches (Haddad and Tewksbury 2005; Trainor et al. 2013; Zeller et al. 2014). Increasingly prohibitive resistance surfaces ( $c = 2$  and  $c = 0.25$ ) may simulate landscape permeability perceived by juveniles in diminished physical



**Fig. 5** Current flow (Ln current) estimates based upon a one to many comparison (where only natal locations are specified as focal nodes) as a function of 3 increasingly prohibitive resistance functions: very non-linear ( $c = 16$ ; **a**), intermediate ( $c = 2$ ; **b**), and approximately linear ( $c = 0.25$ ; **c**) for juvenile Mt. Graham red squirrel dispersal in the Pinaleno Mountains, Arizona USA. Current densities indicate the probability of a random-walking animal using a given cell as it passes through

condition or when extrinsic conditions and internal behavioral states are less conducive to dispersal.

Simulated electrical current traveling between independent source (natal) and ground (settlement) nodes identifies highly connected areas that may promote long distance dispersal movements (Fig. 4). Our longest documented dispersal event was a male that moved 4.9 km (green dispersal vector, Fig. 2), and potential dispersal corridors that may facilitate movements of this magnitude are visible (Fig. 4).

the landscape while moving among focal nodes. We extracted the simulated electrical current at exploration, dispersal, and settlement locations to validate resistance surfaces. Panel **d** shows the mean current density at settlement (*black circles*) and dispersal and exploration locations (*open circles*) for simulated current among natal sites (1: many models), and at dispersal and exploration locations (1:1) for simulated current between natal and settlement locations (1:1 models)

Mean current across all three resistance scenarios provides a connectivity estimate that accounts for individual heterogeneity in perceived landscape permeability and allows for assessment of the placement of fuels reduction treatment blocks established to improve forest health, increase the resiliency of the forest to insect outbreak and fire, and protect and restore remaining MGRS habitat from catastrophic fire (Fig. 4, Panel D; [http://data.ecosystemmanagement.org/nepaweb/nepa\\_project\\_exp.php?project=18628](http://data.ecosystemmanagement.org/nepaweb/nepa_project_exp.php?project=18628)).

Mean simulated current between independent source (natal) and ground (settlement) nodes was relatively low across all fuels reduction treatment blocks (mean:  $-2.28 \pm 0.14$  SD; range  $-2.62$  to  $0.00$ ) which suggests that treatment blocks are well positioned adjacent to high connectivity areas, thereby conserving highly connected habitat by reducing fuel loads in proximal regions (Fig. 4, panel D).

Simulated electrical current traveling among all focal natal nodes (1: many, natal only) provided a way to assess how well our three resistance surfaces facilitated observed exploration, dispersal, and settlement (Fig. 5). We considered the surface with highest simulated electrical current at observed exploration, dispersal and settlement locations as best representing functional landscape permeability for dispersing MGRS. In each scenario, all settlement locations and all but one dispersal and exploration location were included in the connectivity surface, and the most non-linear resistance surface ( $c = 16$ ) resulted in the highest current values at dispersal, exploration, and settlement locations (Fig. 5, panel D), suggesting that this non-linear resistance surface best represented functional landscape permeability for long distance dispersers.

## Discussion

The movements of most small mammal species remain enigmatic (Wikelski et al. 2007; Zeller et al. 2012) yet quantification or estimation of small animal movements is necessary to manage landscapes and support population processes such as natal dispersal. In the Pinaleno Mountains, MGRS habitat is fragmented due to recent tree death and wildfires (Koprowski et al. 2005, 2006; O'Connor et al. 2014), and identification of areas that support natal dispersal movements and gene flow in this endangered population are conservation priorities (U.S. Fish and Wildlife Service 2011). Although we obtained a substantial number of telemetry fixes for MGRS, due to the speed and random timing of long distance dispersal events, very few of these locations were for animals actively engaging in long-distance dispersal movements. However, we show that circuit theory can be useful to estimate potential paths traversed by dispersers from natal area to new territory center as well as assess which resistance surfaces best reflect functional

landscape permeability for long distance dispersers. Such functionality allows us to fill knowledge gaps on small mammal dispersal where robust movement data are lacking and aid in the identification of connected habitat while simultaneously accounting for individual heterogeneity in perceived landscape permeability (McRae et al. 2008; Wade et al. 2015).

One issue with resistance surface connectivity modeling is a lack of empirical or biological evidence applied towards construction of the resistance surface (Zeller et al. 2012; Wade et al. 2015). Resistance surfaces are often based on expert knowledge, or assumed relationships with ecological variables, and often are not validated (Wade et al. 2015; but see LaPoint et al. 2013; St-Louis et al. 2014). We developed three resistance scenarios based upon data from the literature and our own observations of how individuals in different physical condition (Bakker and Van Vuren 2004; Delgado et al. 2010; Debeffe et al. 2012), behavioral state (Dingemanse et al. 2003; Zeller et al. 2014), and definitions of ideal habitat based on natal experience (Stamps 2006; Mabry and Stamps 2008) may be able to access landscape features and be motivated to move. MGRS in good condition with exploratory behavioral phenotypes tend to disperse farther, and juveniles select settlement locations structurally and compositionally similar to their natal area (Merrick and Koprowski 2016a, b).

Based upon our assessments and those of previous research, non-linear resistance functions appear to best represent areas used for prospecting and dispersal movements (Trainor et al. 2013; Zeller et al. 2014, this study). Non-linear resistance surfaces ( $c = 16, 1,$  &  $2$ ) developed for the red-cockaded woodpecker (*Picoides borealis*), an endangered forest obligate, best explained prospecting and dispersal movements for short distance dispersers in an independent validation data set, but not long distance dispersers, which demonstrates that single resistance surfaces should not be used to reflect the dispersal behavior of an entire population (Trainor et al. 2013). Further, a study of context-dependent resource selection, based upon regular GPS fixes at 5 min intervals, revealed that resource selection and estimates of resistance are sensitive to the scale and behavioral state of the animal (Zeller et al. 2014), whereby animals engaged in movement perceive landscape resistance differently compared to the same animals engaged in resource use.



In our study, we were limited in our ability to empirically estimate landscape resistance for long-distance dispersers and subsequently relied upon current flow estimates at a limited subset of telemetry fixes obtained during exploration and long distance dispersal movements. Our simulation of three increasingly prohibitive resistance surfaces (non-linear to linear) allowed us to represent individual heterogeneity in perceptions of landscape permeability within a population. Mean simulated electrical current across three resistance scenarios highlights connected regions potentially important for conservation or restoration while also taking into account heterogeneity in functional landscape permeability (Trainor et al. 2013). Modeling current flow as a one to many function among only natal focal nodes allowed us to assess which resistance scenarios best-reflected functional landscape permeability by a dispersing small mammal. Such models can aid in the identification of areas that promote connectivity in the face of rapid landscape change (McRae et al. 2008; Nuñez et al. 2013).

#### Limitations and future considerations

Despite the advantages of using circuit theory to model functional landscape connectivity for small mammals, we acknowledge some limitations and recognize several assumptions we made in implementing models. Models of probable use depend upon point selection functions developed with locations of animals that we captured, and the scope of inference for all subsequent models of landscape resistance and connectivity are tied to these individuals. However, this method is appropriate to address: (1) what movement paths might individuals in a given study take during long distance dispersal, and (2) which resistance scenarios best represent functional landscape connectivity for the study organism? We assumed that MGRS make similar decisions for movement as in habitat selection, which is not necessarily the case (Wade et al. 2015). Areas that support dispersal movements may not need to be habitat in order to support movement of individuals (Haddad and Tewksbury 2005; LaPoint et al. 2013; Trainor et al. 2013), and dispersing juveniles may be less risk-averse and more likely to cross gaps or low quality forest matrix compared to adults. This would imply that our models of use, resistance, and connectivity are conservative. While we obtained a limited

number of telemetry fixes for animals during active exploration and long distance dispersal movements, our validation efforts support the idea that the dispersers, particularly long distance dispersers, perceive landscape as more permeable compared to settled animals, as the most non-linear and least prohibitive resistance surface ( $c = 16$ ) best reflected current flow to locations animals used during dispersal and exploration as well as for settlement. Finally, although an important factor in population processes like dispersal, we did not include site occupancy or density as fixed effects in our probability of use models. MGRS densities are known to be exceedingly low and we found that inclusion of local density in the natal area did not improve models that predict probability of dispersal and dispersal distance (Merrick and Koprowski 2016a).

As telemetry technology continues to improve via miniaturization and GPS tracking technology, reduced costs, and increased sensitivity of satellites to low-power tags (Wikelski et al. 2007; Recio et al. 2011; Stevenson-Holt et al. 2014), we anticipate a unique opportunity to further validate and refine connectivity models for small mammals.

#### Conclusion

Circuit theory provides a useful tool to model functional landscape connectivity, particularly in cases where actual movement data are lacking or sparse due to rapid, cryptic movement behavior. Circuit theory-based models represent hypotheses about how animals may move through landscapes, react to barriers, and perceive permeability and resistance, both in terms of gene flow over generations (McRae and Beier 2007), and for individuals moving between discrete locations (McRae et al. 2008). Circuit theory models offer improvements over least cost models by identifying multiple candidate movement paths important for species conservation rather than a single least cost path (McRae et al. 2008; Cushman et al. 2013). We show that circuit theory is a useful tool to identify possible small mammal natal dispersal routes, account for individual heterogeneity in functional landscape permeability, and compare resistance scenarios. Twenty five percent of all mammals threatened with extinction, and 52% of mammals with known population data are in decline, including those listed as species of

Least Concern (Schipper et al. 2008). Given global trends in mammal population decline, increased threats of habitat loss and fragmentation (Theobald et al. 2012), and the fact that most mammals are small (~70%; Wikelski et al. 2007), the need to assess functional landscape connectivity from the perspective of small mammals is critical. Our work complements and builds upon previous applications of circuit-theory to animal movement modeling and provides a case study of its applicability to small mammal conservation and management.

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