



## Research

**Cite this article:** Merrick MJ, Koprowski JL. 2016 Evidence of natal habitat preference induction within one habitat type. *Proc. R. Soc. B* **283**: 20162106.  
<http://dx.doi.org/10.1098/rspb.2016.2106>

Received: 24 September 2016

Accepted: 11 October 2016

**Subject Areas:**

behaviour, ecology

**Keywords:**

natal dispersal, natal habitat preference induction, habitat selection, habitat specialist, Arizona

**Author for correspondence:**

Melissa J. Merrick  
 e-mail: [mmerrick@email.arizona.edu](mailto:mmerrick@email.arizona.edu)

Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.fig-share.c.3551304>.

# Evidence of natal habitat preference induction within one habitat type

Melissa J. Merrick and John L. Koprowski

School of Natural Resources and the Environment, Wildlife Conservation and Management, University of Arizona, Tucson, AZ, USA

MJM, 0000-0001-8330-4795

Natal habitat preference induction (NHPI) is a mechanism for habitat selection by individuals during natal dispersal. NHPI occurs in wild animal populations, and evidence suggests it may be a common, although little studied, mechanism for post-dispersal habitat selection. Most tests of NHPI examine the influence of distinct, contrasting natal habitat types on post-dispersal habitat selection. We test the hypothesis that NHPI can occur within a single habitat type, an important consideration for habitat specialists. The Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) is an endangered forest obligate restricted to a single mountain primarily within mixed-conifer forest. We test for NHPI by comparing intra-individual differences in natal and settlement habitat structure and composition to expected random pairwise differences. Dispersing juveniles appear to select settlement locations that are more similar to natal areas than expected in several forest structure and composition variables that include canopy cover and live basal area. Our results provide support for NHPI as a mechanism for post-dispersal habitat selection in habitat specialists that occupy a single vegetation community type.

## 1. Introduction

Natal dispersal is an important ecological process to promote gene flow, reduce inbreeding, and contribute to the viability of populations and survival of individuals [1], and is composed of three distinct phases: emigration, transience, and immigration [2]. Much work is dedicated to understanding the proximate and ultimate factors driving emigration [2–4] and has provided a framework in which we can form and test hypotheses regarding the initiation of natal dispersal. By contrast, fewer studies focus on transience and immigration (settlement), which are difficult to document, yet of critical importance for understanding how individuals select features on the landscape and make settlement decisions. Ultimately choices during these phases influence individual fitness [5–7]. The transience stage of natal dispersal can be costly both in terms of energy expenditure and risk of predation during dispersal, and in deferred costs to survival and fitness post-dispersal [8,9], therefore, strategies to aid in identifying quality settlement locations and reduce time spent in transience may be favoured [10]. A disperser's decision to stop moving and select a settlement location may be among the most important choices made in its lifetime, akin to selecting mates [5,6,10], yet what environmental cues play a role in this decision are poorly understood. Several factors may serve as reliable cues that influence or trigger settlement during natal dispersal, including an individual's physical condition, social cues such as the presence of conspecifics, and environmental cues that signify quality habitat complete with food, shelter, and mates [10,11].

Recognition of and preference for habitat features that resemble those of the natal area by dispersing individuals is termed habitat imprinting or natal habitat preference induction (NHPI) [12–14]. This mechanism for habitat selection is thought to have adaptive significance because a natal area that supports offspring to dispersal age likely typifies quality habitat [15]. Selection may favour NHPI as the use of reliable cues facilitates rapid identification of quality habitat and reduces search time prior to settlement [12], and may reduce the dependence

on specific phenological cues only present during narrow temporal windows. NHPI, in turn, may drive observed variation in post-dispersal habitat selection [12]. Rapid habitat alteration via anthropogenic and climate-driven disturbances may complicate or reduce the current adaptive value of NHPI, effectively decoupling the cues that once conferred fitness benefits. Situations where once reliable habitat cues become decoupled from fitness benefits are known as ecological traps [16–18], and if NHPI is a common mechanism used by dispersers to identify suitable settlement locations, habitat selection may appear maladaptive in landscapes that have experienced rapid change from anthropogenic disturbances such as fire, fragmentation, non-native species, parasites, and disease [18,19]. Further, should rapid change alter important habitat cues without affecting the overall fitness benefits of a site, NHPI may prevent settlers from identifying sites as suitable for occupancy [20]. Thus NHPI is an important consideration for the conservation of threatened species and the habitats required to sustain them.

Evidence of natal habitat preference during dispersal has been documented in insects, fish, amphibians, reptiles, birds, and mammals [11,17]. NHPI has rarely been satisfactorily documented in observational field-based studies due to three strict criteria that must be satisfied: (i) genetic variation in habitat preference must be controlled, (ii) experience with natal environments should occur at the appropriate age or ontogenetic stage that dispersal occurs, and (iii) tests for habitat preference should occur at the age or ontogenetic stage that settlement occurs [12]. Several recent studies appear to document NHPI in wild animal populations, and suggest NHPI may be important. Young North American red squirrels (hereafter red squirrels), Eurasian red squirrels (*Sciurus vulgaris*), brush mice (*Peromyscus boylii*), and red wolves (*Canis rufus*) selected settlement sites of a similar habitat type to their natal area or natal home range [14,21–24]. Siberian flying squirrels (*Pteromys volans*) settled in forest patches of similar size to the natal patch [23], and dispersing common loons (*Gavia immer*) selected lakes of similar size and pH to their natal lake for breeding [25]. Although most tests of NHPI examine post-dispersal habitat selection among distinct, contrasting habitat types, if NHPI is a successful strategy we might also expect that animals have the capacity to resolve more subtle structural or compositional differences within a single habitat type, particularly in the case of habitat specialists.

North American red squirrels are a small forest obligate mammal with a broad distribution and are unique in their territoriality and food hoarding behaviour; territories are centred around a central larder hoard or midden [26]. Because of their close affinity to and habitat specificity within forests [26], red squirrels make excellent model systems for the study of habitat cues that influence settlement decisions. Red squirrel territoriality and larder hoarding behaviour help buffer against fluctuating resource availability, and also require that individuals make informed settlement choices within a narrow window of time, as the chosen settlement location must supply adequate conifer cones and suitable habitat structure to maintain cone stores through the following year. Previous work has shown that red squirrels inhabiting mature and highly thinned mixed-conifer forest exhibit a preference for settlement sites that resemble their natal areas [22]. We studied natal dispersal and post-dispersal habitat selection, and test for evidence of NHPI in the Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) inhabiting mixed-conifer

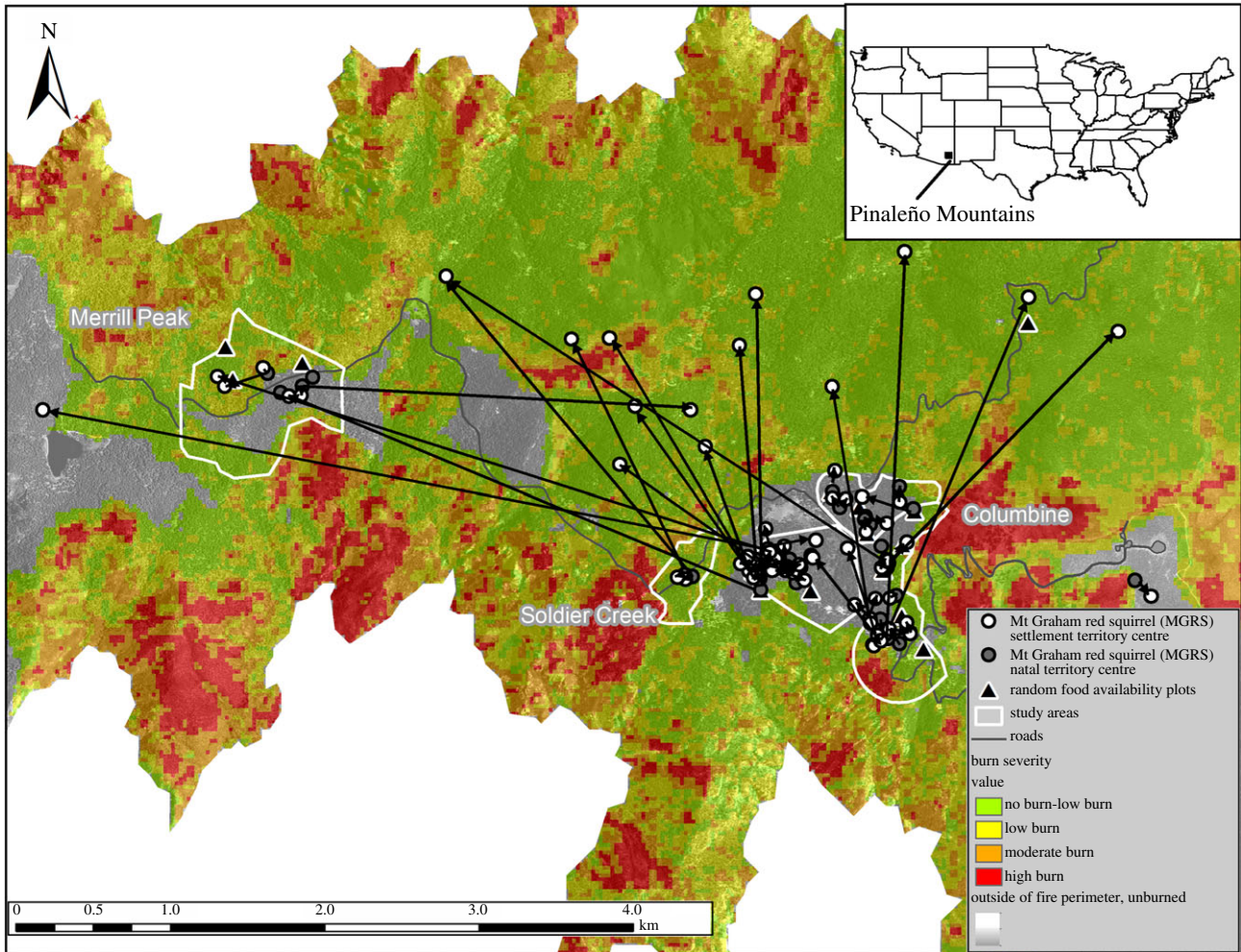
forest by measuring microhabitat variables at two spatial scales. Mt Graham red squirrels are an isolated, endangered subspecies restricted to the Pinaleno Mountains, in southeastern Arizona, USA, and represent the southernmost population of red squirrels in North America [27] (figure 1). Recent genetic analyses suggest that southwestern *Tamiasciurus* belong to a separate species *T. fremonti* [28], further distinguishing Mt Graham red squirrels genetically from other red squirrel populations in which NHPI has been investigated. The Mt Graham red squirrel is uniquely suited to study NHPI and its influence on habitat use and selection for many reasons: (i) Mt Graham red squirrels (hereafter red squirrels) are intensively monitored via mark–recapture, radiotelemetry, and population surveys, hence many individuals of known age are followed during the period when both dispersal and settlement are known to occur, (ii) recent analyses of nuclear and mitochondrial DNA indicate that little genetic variation exists, with mean inter-individual relatedness = 0.75 [27,29], which may allow us to more adequately disentangle the influence of genetics or NHPI on inter-individual differences in habitat selection observed in the field [12], (iii) recent disturbance events including insect infestation beginning in 1996 [30] and subsequent wildfires in 1996 and 2004 [31] have altered forest composition and continuity, in some areas leaving structure intact, but substantially reducing living biomass, and (iv) despite high mortality and reduced reproductive success in insect damaged spruce–fir forest, red squirrel settlement cues appear to remain unchanged, suggesting a potential ecological trap for individuals that settle there [16,32,33].

If NHPI occurs in juvenile red squirrels born and settling within mixed-conifer forest, then intra-individual differences in forest structure and composition between natal and settlement locations should be less than that expected from random pairwise comparisons of natal and settlement sites. We determined natal and post-dispersal site characteristics from ground-based plots and remotely sensed data at two spatial scales and assessed habitat selection in juveniles by comparing forest structure, composition, food availability, and microclimate at natal and settlement sites to random locations. We then tested for evidence of NHPI within mixed-conifer forest across all individuals and in short- versus long-distance dispersers by quantification of intra-individual differences in forest structure and composition between natal and settlement locations compared with expected differences obtained from randomization.

## 2. Material and methods

### (a) Study area

Our study area comprised vegetation communities of mesic mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*), southwestern white pine (*Pinus strobiformis reflexis*), white fir (*Abies concolor*), cork bark fir (*Abies lasiocarpa* var. *arizonica*), Engelmann spruce (*Picea engelmannii*), quaking aspen (*Populus tremuloides*), and high-elevation spruce–fir forest dominated by cork bark fir and Engelmann spruce [31,34]. Animals for this study were captured primarily within three mesic mixed-conifer forest study sites: Columbine (104.3 ha), Soldier Creek (14.7 ha), and Merrill Peak (72.2 ha; figure 1). Red squirrel habitat in the Pinaleno Mountains occurs above 2591 m, and animals in our study used habitat between 2647 and 3267 m in elevation. Fires in 1996 and 2004 burned a combined 14160 ha of pine, mixed-conifer, and spruce–fir forest (45% of the forest



**Figure 1.** Overview of Mt Graham red squirrel habitat above 2 348 m in elevation, burn severity and associated study areas in the Pinaleno Mountains, Arizona, USA. Natal and settlement sites obtained from radio-collared juveniles shown in grey and white circles, respectively, and straight-line dispersal vectors are indicated by black lines.

above 2 135 m) which, combined with tree death from insects, reduced spruce and cork bark fir area by 66% [31].

### (b) Tracking dispersal and settlement

Between May 2010 and February 2014, we trapped, radio-collared and followed 94 juvenile red squirrels through dispersal, settlement, and post-settlement. To find and capture juveniles, we tracked and monitored the location and reproductive condition of adult females radio-collared as part of a long-term study to investigate red squirrel space use [35]. Whenever we documented a lactating adult female, we observed her nest a minimum of once per week for 2–4 h time blocks until juvenile emergence. Following emergence of juveniles from the nest, we set live traps (Tomahawk Live Trap, Tomahawk, WI, USA: model no. 201) around the natal nest and midden between 06.00 and 18.00 h to capture as many juveniles per litter as possible. We checked traps at least once per hour. Upon capture, we transferred each individual to a cloth handling cone [36] to measure morphological traits, apply unique marks, and fit radio collars (SOM 2190, Wildlife Materials International) [35]. To reduce radio-collar weight, we used transmitters attached to a thin (3 mm) plastic neck band and to allow for growth we added a 3 × 20 mm strip of thin, compressible foam mounting tape affixed to the inside of the neck band (total weight = 5 g). We recaptured individuals at least every three months to measure growth and check radio-collar fit.

We used radiotelemetry to track juvenile red squirrel movements from capture to settlement, locating each juvenile a

minimum of 12 times each month until settlement or the animal died or disappeared from our study area. When an animal's radio-collar signal disappeared from the natal area, we initiated a three-step response: (i) observe and trap for the individual at the natal nest and midden in the event that the radio collar had stopped functioning, (ii) drive accessible roads within red squirrel habitat to traverse the length of the mountain range, with frequent stops to detect signals, and (iii) hike an 8 km trail loop to listen for signals regularly. We repeated this process weekly until the animal was found or, if not located, was considered to be missing by December of a given year. All long-distance dispersers ( $n = 33$ ) and several animals with off-air transmitters were relocated via the three-step process; 17 animals were never relocated. We monitored all known-fate individuals for signs of settlement that included conifer cone caching at a central midden and territorial vocalizations indicating territory ownership [37]. Following settlement, we continued to monitor individual space use and survivorship throughout each individual's lifetime. We measured straight-line dispersal distance from the natal nest where a juvenile was known to have emerged to the territory centre (midden) where it settled.

### (c) Forest structure and composition at natal and settlement locations

We measured forest structure, composition, food availability, and microclimate via ground-based plots and lidar (light detection and ranging) remotely sensed data at two spatial scales to:

(i) examine natal and settlement habitat compared with random locations and (ii) to test for evidence of NHPI in red squirrels based upon intra-individual differences in forest structure and composition at natal and settlement locations (see electronic supplementary material, S1). We characterized forest around natal and settlement locations at plot level (30 m radius) and home range scales (100 m radius). At ground-based plots we recorded tree species, diameter at breast height (dbh; cm), whether a tree was alive or dead, summarized living, dead, and large trees >40 cm dbh, calculated total and live basal area (square metres per hectare), calculated tree species diversity indices (Shannon's  $H$  and Simpson's  $D$ ) [38], and estimated cone production if the conifer was alive via a cone index (log (estimated cones per ha)). We collected plot data at emergence locations for 58 individuals, settlement locations for 50 individuals, and had data to compare forest characteristics of natal and settlement locations for 47 individuals.

For remotely sensed plot and home range scale habitat measurements, we generated 30 and 100 m radius buffers around natal nests and settlement middens for 63 individuals that successfully settled. Within each buffer, we summarized six lidar-derived forest structural variables (25 m pixel resolution) [39]: per cent canopy cover, live and total basal area (square metres per hectare), mean tree height (m), standard deviation in tree height, and the living to total basal area ratio. We summarized the mean pixel value for underlying lidar-derived raster layers within 30 and 100 m buffers.

#### (d) Evidence of natal habitat preference induction within mixed-conifer forest

We tested the hypothesis that forest structure and composition are more similar between natal and settlement locations for an individual red squirrel compared with random pairwise comparisons between natal and settlement sites. We followed Piper *et al.* [25] and calculated the intra-individual Euclidean distance (dist, R Core Team 2015;  $\sqrt{(\sum(x_i - y_i)^2)}$ ) between scaled, centred forest structure and composition vectors measured at natal and settlement locations via ground-based plots ( $n = 47$ ) and via lidar summarized within 30 and 100 m buffers ( $n = 63$ ). We compared the mean of intra-individual Euclidean distances between natal and settlement habitat vectors calculated from each dataset (ground-based plots, lidar data within 30 and 100 m buffers) to the mean expected Euclidean distance obtained from 10 000 randomizations of pairings between natal and settlement habitat vectors. To test whether intra-individual differences in forest composition between natal and settlement sites were smaller than expected (i.e. sites were more similar than expected), we calculated the proportion of Euclidean distances from random natal-settlement site pairings that were smaller than the mean observed intra-individual Euclidean distance. We considered a mean intra-individual Euclidean distance less than 95% of the mean calculated from 100 000 randomizations of natal-settlement pairings as evidence in support of NHPI. To test for evidence of NHPI in short- versus long-distance dispersers, we subdivided each dataset (ground-based plot, 30 and 100 m buffers) by dispersal distance. A natural break occurred in dispersal distances between 149 and 200 m, and 147 m is also the average diameter of adult female home ranges during autumn when young are dispersing, so we used 150 m as a cut-off between short-distance dispersers that settled within or adjacent to their mother's territory (less than 150 m) and long-distance dispersers (greater than or equal to 150 m).

To assess which forest structure and composition variables are more similar between natal and settlement locations than expected and might, therefore, contribute most to NHPI, we repeated the above comparisons for each variable separately. Instead of simultaneously comparing data vectors of all variables

measured at natal and settlement sites via Euclidean distance, we calculated the observed mean intra-individual difference between natal and settlement sites for each variable and compared this value with the mean expected difference between natal and settlement sites for a given variable obtained from 100 000 randomizations of the dataset. We evaluated the observed versus expected intra-individual differences in forest structure and composition variables for all animals, and in long-distance dispersers.

We tested for the influence of seven individual or environmental attributes on intra-individual Euclidean distance scores between natal and settlement sites: individual body mass index (body mass at capture/days since birth), number of litter mates, individual behavioural tendency for locomotion [40], dispersal distance, cone availability at the natal site, cone availability at the settlement site, and year. We used R v. 3.1.1 ([www.r-project.org](http://www.r-project.org)) for all statistical analyses with a specified  $\alpha = 0.05$  unless noted otherwise.

### 3. Results

#### (a) Tracking dispersal and settlement

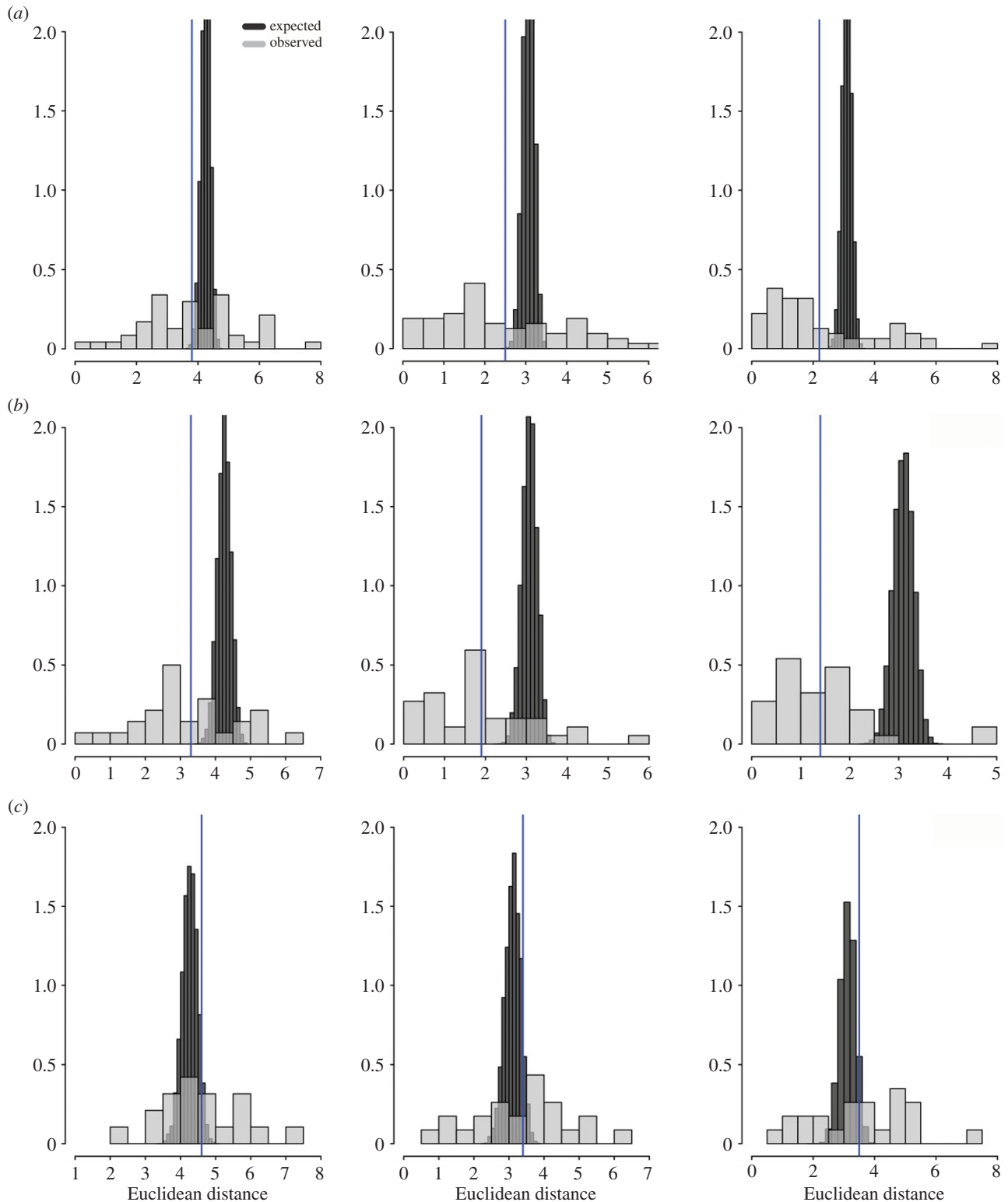
Of the 94 juvenile red squirrels radio-collared between 2010 and 2013, 63 survived and were successfully tracked to settlement locations (29 females, 34 males). Combined with known dispersal distances of marked animals incidentally recaptured as adults from previous years ( $N = 11$ ), we quantified dispersal distance for 74 individuals. Mean straight-line dispersal distance for red squirrels ( $\pm$  s.d.) was  $679.8 \pm 1067.7$  m, with juvenile males dispersing farther than females (mean dispersal distance: males =  $969.4 \pm 1224.8$  m; females =  $339.0 \pm 726.4$  m; Welch  $t_{64,8} = -2.4$ ,  $p = 0.02$ ). Mean estimated date of settlement for red squirrels during our study (2010–2013) was day 272 of a 365 day calendar year, or 29 September—the earliest observed settlement date was 5 August, the latest was 5 December. We excluded settlement dates for three individuals that did not settle the year of their birth but remained transient until successfully obtaining their own territories the following spring. Juvenile red squirrels in this study were captured in mixed-conifer forest with the exception of one individual from previous years captured in spruce–fir forest [41], and all mixed-conifer born individuals tracked between 2010 and 2013 settled in mixed-conifer forest; the one individual born in spruce–fir forest settled in spruce–fir forest.

#### (b) Forest structure, composition, food, and microclimate

We found evidence of selection for several forest structure and compositional features known to be important for red squirrels and associated with dependable food and shelter and maintenance of a microclimate suitable for conifer cone storage [32,34]. In general, natal and settlement sites were more similar to each other and differed from random sites (electronic supplementary material).

#### (c) Evidence of natal habitat preference induction in mixed-conifer forest

Across plot types, intra-individual differences in forest structure and composition, estimated simultaneously via Euclidean distance between natal and settlement habitat



**Figure 2.** Distribution of observed and expected intra-individual Euclidean distance scores between forest structure and composition at natal and settlement sites for juvenile Mt Graham red squirrels in the Pinaleno Mountains, Arizona, USA. Intra-individual Euclidean distance scores within 30 m ground-based plots, and within 30 and 100 m buffers summarized via lidar data are shown in relation to 10 000 iterations of randomized pairwise comparisons between natal and settlement sites for all animals (a), short-distance dispersers (b), and long-distance dispersers (c). Mean empirical intra-individual Euclidean distances between natal and settlement locations are indicated with a vertical line. (Online version in colour.)

vectors, were smaller than expected based upon randomized pairwise differences (mean Euclidean distance score (ED score) plot ( $n = 47$ ) = 3.8, mean expected ED score of randomizations = 4.2,  $p = 0.002$ ; mean ED score 30 m buffer ( $n = 63$ ) = 2.5, mean expected ED score of randomizations = 3.1,  $p < 0.001$ ; mean ED score 100 m buffer ( $n = 63$ ) = 2.2, mean expected ED score of randomizations = 3.1,  $p < 0.001$ ; figure 2). Intra-individual Euclidean distances were also

smaller than expected in short-distance dispersers (less than or equal to 150 m from their natal nest) across all plot types (mean ED score plot ( $n = 27$ ) = 3.3, mean expected ED score of randomizations = 4.3,  $p < 0.001$ ; mean ED score 30 m buffer ( $n = 37$ ) = 1.9, mean expected ED score of randomizations = 3.1,  $p < 0.001$ ; mean ED score 100 m buffer ( $n = 37$ ) = 1.4, mean expected ED score of randomizations = 3.1,  $p < 0.001$ ; figure 2).

Individuals that dispersed long distances (greater than 150 m from their natal nest) did not exhibit strong evidence of NHPI when all variables were considered simultaneously, as intra-individual Euclidean distances between natal and settlement sites were not different from the expected distribution of random pairwise differences (mean long-distance ED score plot ( $n = 19$ ) = 4.6, mean expected long-distance ED score of randomizations = 4.3,  $p = 0.94$ ; mean long-distance ED score 30 m buffer ( $n = 23$ ) = 3.4, mean expected long-distance ED score of randomizations = 3.1,  $p = 0.91$ ; mean long-distance ED score 100 m buffer ( $n = 23$ ) = 3.5, mean expected long-distance ED score of randomizations = 3.1,  $p = 0.94$ ; figure 2). Each year, 40% of females and 65% of males dispersed greater than 150 m from the natal area. Across scales and methods to summarize forest structure and composition (ground-based plot and 30 and 100 m buffers with lidar data), on average 38% (37% based on ground plot variables, 43% based on lidar variables within 30 m buffers, and 35% based on lidar variables within 100 m buffers) of these individuals did show evidence of NHPI and selected settlement locations that were more similar than expected (i.e. proportion of long-distance dispersers with ED score < random ED score), whereas 62% of long-distance dispersers settled in areas structurally and compositionally dissimilar to their natal area.

There is some evidence that females tended to select settlement sites that were more similar to their natal areas compared with males, particularly at the 30 m scale (ground-based plot mean female ED score: 3.39, mean male ED score 4.17, Welch  $t_{44.9} = -1.77$ ,  $p = 0.08$ ; lidar 30 m buffer mean female ED score: 2.00, mean male ED score 3.01, Welch  $t_{53.8} = -2.54$ ,  $p = 0.01$ ), including ground-based plot variables for females that dispersed long distances (long-distance ground-based plot mean female ED score: 3.66, mean male ED score: 4.93, Welch  $t_{2.8} = -2.51$ ,  $p = 0.09$ ). There were no differences in ED scores between males and females at 100 m buffer scales.

### (i) Evidence of natal habitat preference induction in plot-based and lidar-derived variables

Across all individuals, basal area, live basal area, dead basal area, number of living trees, and species diversity measured at ground-based plots were more similar between natal and settlement locations than expected (table 1). However, when only long-distance dispersers were considered, natal and settlement sites were not different from expected random pairwise differences based upon ground-based plot variables (table 1). Among lidar-derived variables summarized at the plot and home range scale (30 and 100 m buffers), canopy cover, tree height, live basal area, total basal area, variability in tree height, and the ratio of living to total basal area were more similar between natal and settlement locations than expected at the home range scale (table 1). Long-distance dispersers settled in locations that had canopy cover and live basal area more similar to their place of birth than expected at the plot scale; at the home range scale canopy cover tended to be more similar than expected approximately 80% of the time (table 1).

Although natal and settlement locations were more similar than expected for many variables, matching was not exact, and mismatches tended to occur such that natal forest variables > settlement forest variables and individuals

settled in locations with less forest structure than their natal area. At ground-based plots, mean intra-individual differences (natal – settlement) suggest that all individuals and long-distance dispersers settled at locations with less basal area, large trees and species richness, more live and dead trees, and higher species diversity compared with their natal area (indicated by sign of actual differences, table 1). For lidar-derived variables summarized at the plot scale, all individuals and long-distance dispersers tended to settle at locations with less canopy cover, mean tree height, variability in tree height, and basal area compared with their natal area. At the home range scale, all individuals and long-distance dispersers settled at locations with more canopy cover and lower mean tree height, variability in tree height, and live to total basal area ratio compared with their natal area; long-distance dispersers settled in areas with more total basal area (table 1).

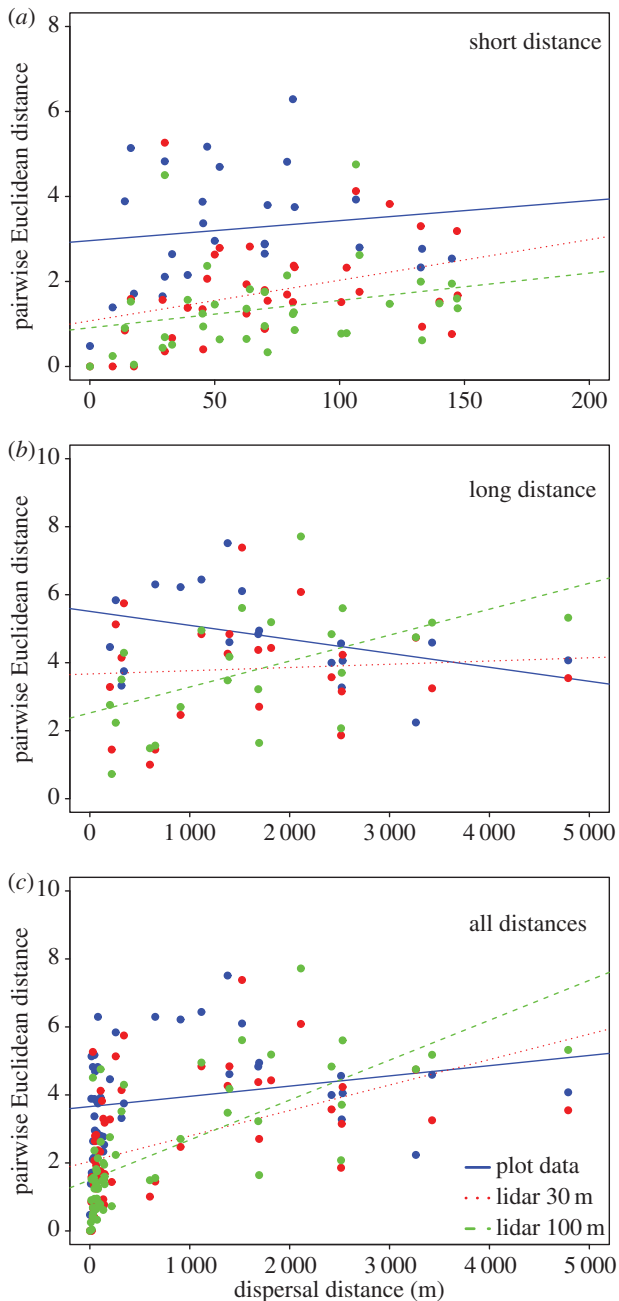
### (ii) Euclidean distance scores versus individual and environmental variables

At ground-based plots, and within 30 and 100 m buffers characterized via lidar, intra-individual ED scores between natal and settlement locations across all animals and for short- and long-distance dispersers were not correlated with individual or environmental attributes such as sex, individual body mass index, number of litter mates, individual behavioural tendency for locomotion, cone availability at the natal site, cone availability at the settlement site, or year (all Pearson's linear correlations,  $p > 0.12$ ; range 0.12–0.72). Intra-individual ED scores between natal and settlement locations were correlated with dispersal distance, and the strength and direction of the correlation depended upon the scale (30 m plot or 100 m home range) and the group of individuals in consideration (all, short-, and long-distance dispersers; figure 3).

For short-distance dispersers, intra-individual ED scores tended to be positively correlated with dispersal distance (ground-based plot:  $r = 0.14$ ,  $p = 0.50$ ; lidar 30 m buffer:  $r = 0.35$ ,  $p = 0.04$ ; lidar 100-m buffer:  $r = 0.27$ ,  $p = 0.11$ ; figure 3). For long-distance dispersers, ED scores at the plot scale tended to be negatively correlated with dispersal distance, evidence that individuals that dispersed the farthest settled at locations more similar to their natal area in terms of variables measured at the plot scale (ground-based plot:  $r = -0.34$ ,  $p = 0.10$ ; lidar 30 m buffer:  $r = 0.07$ ,  $p = 0.74$ ). At the home range scale, ED scores tended to be positively correlated with dispersal distance (lidar 100 m buffer:  $r = 0.53$ ,  $p = 0.01$ ; figure 3). When we considered all animals together, intra-individual ED scores tended to be positively correlated with dispersal distance overall (ground-based plot:  $r = 0.22$ ,  $p = 0.13$ ; lidar 30 m buffer:  $r = 0.47$ ,  $p < 0.001$ ; lidar 100 m buffer:  $r = 0.71$ ,  $p < 0.001$ ; figure 3). In summary, we observed different kinds of evidence in support of NHPI for short- and long-distance dispersers. Intra-individual natal and settlement habitat characteristics were most similar among short-distance dispersers (figure 2), but habitat similarity may be partially explained by spatial autocorrelation (figure 3). Among long-distance dispersers at the plot scale, lack of spatial autocorrelation in post-settlement habitat selection and sustained evidence of NHPI for key red squirrel habitat components provide further evidence for NHPI despite the influence of spatial autocorrelation.

**Table 1.** Observed versus expected absolute differences in forest structure and composition between natal and settlement locations for juvenile Mt Graham red squirrels measured from ground-based plots and lidar data within 30 and 100 m buffers. Shown are the absolute differences in forest structure and composition at settlement locations compared with natal locations (natal – settlement, with sign of the actual difference indicated by +/–) for all animals and for long-distance dispersers that settled >150 m from the natal area survival to first spring in the Pinaleno Mountains, Arizona, USA. Instances where observed differences were less than expected with probability  $p < 0.2$  are in italics to indicate variables that may represent important cues for NHP1.

plot variables	natal – settlement, all			natal – settlement, long-distance dispersers				
	(observed difference)	+/–	expected difference	<i>p</i> -value (obs < exp)	(observed difference)	+/–	expected difference	<i>p</i> -value (obs < exp)
basal area	28.00	+	36.00	<i>0.005</i>	40.00	+	36.00	0.820
live basal area	23.00	+	29.00	<i>0.008</i>	34.00	+	32.00	0.700
dead basal area	13.00	+	15.00	<i>0.029</i>	15.00	+	15.00	0.550
live trees/ha	160.00	–	196.00	<i>0.017</i>	220.00	–	211.00	0.610
dead trees/ha	117.00	–	133.00	<i>0.076</i>	150.00	–	134.00	0.790
large live trees/ha	72.00	+	72.00	0.500	94.00	+	78.00	0.940
live : total basal area	0.15	–	0.13	0.940	0.14	–	0.13	0.630
species richness	1.10	+	1.20	<i>0.170</i>	1.40	+	1.40	0.360
Shannon's <i>H</i>	0.28	–	0.34	<i>0.036</i>	0.37	–	0.35	0.620
Simpson's <i>D</i>	0.12	–	0.15	<i>0.018</i>	0.17	–	0.15	0.830
lidar 30 variables								
canopy cover (%)	7.10	+	10.00	<i>0.000</i>	9.10	+	11.00	<i>0.040</i>
tree height (m)	2.10	+	2.50	<i>0.013</i>	3.40	+	2.70	0.980
s.d. tree height	0.96	+	1.00	<i>0.120</i>	1.60	+	1.20	1.000
live basal area	6.70	+	10.00	<i>0.000</i>	10.00	+	12.00	<i>0.100</i>
basal area	14.00	+	17.00	<i>0.006</i>	24.00	+	19.00	0.990
live : total basal area	0.09	+	0.11	<i>0.048</i>	0.15	+	0.13	0.830
lidar 100 variables								
canopy cover (%)	4.90	–	8.80	<i>0.000</i>	7.50	–	8.20	<i>0.210</i>
tree height (m)	1.40	+	1.90	<i>0.000</i>	2.70	+	2.10	1.000
s.d. tree height	0.65	+	0.77	<i>0.014</i>	1.10	+	0.93	0.960
live basal area	4.60	+	8.30	<i>0.000</i>	7.70	+	7.70	0.510
basal area	9.70	+	13.00	<i>0.000</i>	17.00	–	13.00	0.990



**Figure 3.** Relationship between intra-individual pairwise Euclidean distance scores between natal and settlement sites for juvenile Mt Graham red squirrels in the Pinaleno Mountains, Arizona, USA, and dispersal distance (m) for short-distance dispersers  $\leq 150$  m (a), long-distance dispersers moving  $> 150$  m (b), and all animals (c). Lines represent linear models of the relationship between Euclidean distance scores and dispersal distance at three scales of forest structure and composition characterization: ground-based plot data (solid line), lidar data summarized within 30 m buffers (dotted line), and lidar data summarized within 100 m buffers (dashed line). (Online version in colour.)

## 4. Discussion

Red squirrels appear to select forest structure and composition that differs from that randomly available on the landscape, and individuals tend to select components of forest structure that resemble their own natal area. Evidence for NHPI has been documented in free-living mammals born in strongly contrasting vegetation communities or structural types such as woodland and prairie [42], grassland and oak savannah [14], an urban, forest, shrub, and agricultural matrix [24], or in

thinned versus mature forest [22], and here we test the hypothesis that NHPI may also function in single vegetation communities occupied by habitat specialists. Our results provide additional support for NHPI as a mechanism for post-dispersal habitat selection [14,22,25,42], in general, and specifically in an organism that is dependent upon particular vegetation community types such as mixed-conifer forest.

### (a) Evidence for robustness of natal habitat preference induction in mixed-conifer forest

Forest structure and composition attributes important for red squirrel survival and reproduction at natal and settlement sites were more similar for individuals than expected based upon random pairwise comparisons when all animals and short-distance dispersers are considered. Positive correlations between intra-individual Euclidean distance scores and dispersal distance could suggest that observed similarities between natal and settlement sites are due to spatial autocorrelation alone and not NHPI [25]. However, negative correlations between intra-individual Euclidean distance scores and dispersal distance in long-distance dispersers at the plot scale provides evidence that dispersers moving through unfamiliar terrain may rely more on NHPI for post-dispersal habitat selection, and Mt Graham red squirrels tend to select settlement sites at the plot rather than home range scale. Further, selection for post-settlement habitat characteristics that resemble the natal area may be strongest among females. The Pinaleno Mountains are heterogeneous in terms of topography and vegetation structure as a result of variable microclimate and past disturbance events [31], and the majority (66%) of individuals in this study were born in small (less than 30 ha) forest patches [40]. Short- and long-distance dispersers settled in a mean distance of 71 and 1638 m from their natal areas, respectively. Such distances are the edge of the mother's home range for short-distance dispersers, thus the majority of juvenile red squirrels encountered heterogeneity in forest structure and composition while prospecting for a place to settle. Further, we show that all individuals settle in locations that have similar canopy cover and live basal area to their natal area at the plot and home range scale, regardless of dispersal distance. NHPI within a single vegetation community type may depend upon simple cues that provide a baseline for assessing habitat quality.

### (b) Natal habitat preference induction and implications for rapidly changing landscapes

Whether NHPI is an adaptive strategy for post-dispersal habitat selection following disturbance events depends upon what cues are used to represent quality habitat and the reliability of those cues following disturbance events. If individuals rely primarily on structural cues, recent or future disturbances such as defoliation, disease, and fire may leave key structural components intact, but significantly alter the fitness benefits once coupled with structure such as food availability and shelter, a potential ecological trap [19,33,43,44]. Ecological traps tend to be associated with human-induced rapid environmental change (or HIREC) as these changes are sudden and beyond the purview of conditions organisms have experienced over evolutionary time [17,45]. However, some organisms' behavioural responses to HIREC are more flexible than others and behavioural plasticity in response to novel habitat cues, in



conjunction with habitat specificity may be key factors in determining the current adaptive value of NHPI [44]. In the case of red squirrels in the Pinaleno Mountains, cuing in on canopy cover and living basal area may allow individuals to avoid ecological traps when settling in mixed-conifer forests. While NHPI as a mechanism for post-dispersal habitat selection has potential to be maladaptive in the face of HIREC [17,44], the process may also be a key strategy that allows naive young animals to find patches of habitat within an unsuitable matrix, and reduces the costs associated with all phases of dispersal [8,9,46].

### (c) Natal habitat preference induction as a consideration for management and recovery

NHPI influences post-dispersal habitat selection, and recognition of NHPI may aid in the management of habitat and individual animals to maximize recovery, reintroduction, or translocation efforts. Despite efforts to identify and set aside quality habitat for species conservation and recovery, limited recruitment or reduced fitness is sometimes observed [17,20,25,45]. NHPI may be one mechanism behind such apparent mismatches, or the rapid movement of translocated animals from release sites [13,47] as individuals do not recognize suitable habitat as such due to the lack of one or more important settlement cues [20]. For populations born in habitat that is declining in quality, NHPI may drive habitat selection inertia [25] that may need to be overcome, otherwise selection for cues from degraded habitat could lead to an ecological trap [17]. Thus, NHPI may be an important consideration for implementing habitat improvement or restoration projects. Habitat restoration projects, in turn, provide excellent opportunities to test NHPI.

We provide evidence that settlement by a habitat specialist is influenced by components of habitat structure in the natal

area, providing further support for NHPI in free-living animals. This study contributes to a growing literature serving to improve our current understanding of mechanisms for habitat selection and settlement [12,14,21,25], and highlights the fact that our best conservation efforts may not be successful without considering such mechanisms [13].

**Ethics.** All fieldwork was conducted under the University of Arizona Institutional Animal Care and Use Committee protocol no. 08-024, Arizona Game and Fish Department scientific collecting permit no. SP654189, US Fish and Wildlife Service permit no. TE041875-0, and adhered to the American Society of Mammalogists guidelines for the use of wild mammals in research (Sikes, Gannon, and The Animal Care and Use Committee of the American Society of Mammalogists 2011).

**Data accessibility.** Merrick M, Koprowski J. Data from: Evidence of natal habitat preference induction within one habitat type. Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.v087b>.

**Authors' contributions.** M.J.M. and J.L.K. jointly conceived the study. M.J.M. carried out the data collection, analysis, and drafting of the manuscript. J.L.K. provided additional funding, logistical support, served as project advisor, and contributed to manuscript revisions.

**Competing interests.** We declare we have no competing interests.

**Funding.** This research was supported by grants from the University of Arizona, US Fish and Wildlife Service, USDA Forest Service, Arizona Game and Fish Department, the Arizona Agricultural Experiment Station to J.L.K. and funds to M.J.M. from The Joint Fire Sciences Program Graduate Research Innovations award no. 3005940, The University of Arizona NASA Space Grant Consortium Fellowship, The University of Arizona Institute of the Environment Carson Scholars Fellowship, The American Society of Mammalogists Grant in Aid of Research and ASM Fellowship, The American Museum of Natural History Theodore Roosevelt Graduate Student Research Award, The Southwestern Association of Naturalists Howard McCarley Student Research Award, and T & E Inc. Grants for Conservation Biology.

**Acknowledgements.** We thank the Mt Graham Red Squirrel Research Programme for assistance in the field. This manuscript was improved by comments from R. W. Mannan, C. Conway, and two anonymous reviewers.

## References

- Gaines MS, McClenaghan LR. 1980 Dispersal in small mammals. *Annu. Rev. Ecol. Syst.* **11**, 163–196. (doi:10.1146/annurev.es.11.110180.001115)
- Stenseth NC, Lidicker WZ. 1992 *Animal dispersal: small mammals as a model*. New York, NY: Springer Science & Business Media Dordrecht.
- Holekamp KE. 1986 Proximal causes of natal dispersal in Belding's ground squirrels (*Spermophilus beldingi*). *Ecol. Monogr.* **56**, 365–391. (doi:10.2307/1942552)
- Holekamp KE, Sherman PW. 1989 Why male ground squirrels disperse. *Am. Sci.* **77**, 232–239.
- Mabry KE, Stamps JA. 2008 Searching for a new home: decision making by dispersing brush mice. *Am. Nat.* **172**, 625–634. (doi:10.1086/591682)
- Selonen V, Hanski IK. 2009 Decision making in dispersing Siberian flying squirrels. *Behav. Ecol.* **21**, 219–225. (doi:10.1093/beheco/arp179)
- Weins JA. 2001 The landscape context of dispersal. In *Dispersal* (eds J Clobert, E Danchin, AA Dhont, JD Nichols), p. 452. New York, NY: Oxford University Press.
- Stamps JA, Krishnan VV, Reid ML. 2005 Search costs and habitat selection by dispersers. *Ecology* **86**, 510–518. (doi:10.1890/04-0516)
- Bonte D *et al.* 2011 Costs of dispersal. *Biol. Rev. Camb. Philos. Soc.* **87**, 290–312. (doi:10.1111/j.1469-185X.2011.00201.x)
- Stamps J, Davis J. 2006 Adaptive effects of natal experience on habitat selection by dispersers. *Anim. Behav.* **72**, 1279–1289. (doi:10.1016/j.anbehav.2006.03.010)
- Fletcher RJ. 2007 Species interactions and population density mediate the use of social cues for habitat selection. *J. Anim. Ecol.* **76**, 598–606. (doi:10.1111/j.1365-2656.2007.01230.x)
- Davis JM, Stamps JA. 2004 The effect of natal experience on habitat preferences. *Trends Ecol. Evol.* **19**, 411–416. (doi:10.1016/j.tree.2004.04.006)
- Stamps JA, Swaisgood RR. 2007 Someplace like home: experience, habitat selection and conservation biology. *Appl. Anim. Behav. Sci.* **102**, 392–409. (doi:10.1016/j.applanim.2006.05.038)
- Mabry KE, Stamps JA. 2008 Dispersing brush mice prefer habitat like home. *Proc. R. Soc. B* **275**, 543–548. (doi:10.1098/rspb.2007.1541)
- Stamps J, Luttbeg B, Krishnan VV. 2009 Effects of survival on the attractiveness of cues to natal dispersers. *Am. Nat.* **173**, 41–46. (doi:10.1086/593306)
- Schlaepfer MA, Runge MC, Sherman PW. 2002 Ecological and evolutionary traps. *Trends Ecol. Evol.* **17**, 474–480. (doi:10.1016/S0169-5347(02)02580-6)
- Battin J. 2004 When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conserv. Biol.* **18**, 1482–1491. (doi:10.1111/j.1523-1739.2004.00417.x)
- Robertson BA, Hutto RL. 2006 A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* **87**, 1075–1085. (doi:10.1890/0012-9658(2006)87[1075:AFFUET]2.0.CO;2)
- Schlaepfer MA, Sherman PW, Blossey B, Runge MC. 2005 Introduced species as evolutionary traps. *Ecol. Lett.* **8**, 241–246. (doi:10.1111/j.1461-0248.2005.00730.x)

20. Gilroy JJ, Sutherland WJ. 2007 Beyond ecological traps: perceptual errors and undervalued resources. *Trends Ecol. Evol.* **22**, 351–356. (doi:10.1016/j.tree.2007.03.014)
21. Haughland DL, Larsen KW. 2004 Exploration correlates with settlement: red squirrel dispersal in contrasting habitats. *J. Anim. Ecol.* **73**, 1024–1034. (doi:10.1111/j.0021-8790.2004.00884.x)
22. Haughland DL, Larsen KW. 2004 Ecology of North American red squirrels across contrasting habitats: relating natal dispersal to habitat. *J. Mammal.* **85**, 225–236. (doi:10.1644/BWG-113)
23. Selonen V, Hanski IK, Desrochers A. 2007 Natal habitat-biased dispersal in the Siberian flying squirrel. *Proc. R. Soc. B* **274**, 2063–2068. (doi:10.1098/rspb.2007.0570)
24. Karlin M, Chadwick J. 2012 Red wolf natal dispersal characteristics: comparing periods of population increase and stability. *J. Zool.* **286**, 266–276. (doi:10.1111/j.1469-7998.2011.00876.x)
25. Piper WH, Palmer MW, Banfield N, Meyer MW. 2013 Can settlement in natal-like habitat explain maladaptive habitat selection? *Proc. R. Soc. B* **280**, 20130979. (doi:10.1098/rspb.2013.0979)
26. Steele MA. 1998 *Tamiasciurus hudsonicus*. *Mamm. Species* **586**, 1–9. (doi:10.1890/0012-9623(2004)85[22b:ASOMTA]2.0.CO;2)
27. Sanderson HR, Koprowski JL. 2009 *The last refuge of the Mt. Graham red squirrel: the ecology of endangerment*. Tucson, AZ: The University of Arizona Press.
28. Hope AG, Malaney JL, Bell KC, Salazar-Miralles F, Chavez AS, Barber BR, Cook JA. 2016 Revision of widespread red squirrels (genus: *Tamiasciurus*) highlights the complexity of speciation within North American forests. *Mol. Phylogenet. Evol.* **100**, 170–182. (doi:10.1016/j.ympev.2016.04.014)
29. Fitak RR, Koprowski JL, Culver M. 2013 Severe reduction in genetic variation in a montane isolate: the endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*). *Conserv. Genet.* **14**, 1233–1241. (doi:10.1007/s10592-013-0511-x)
30. Koprowski JL, Alanen MI, Lynch AM. 2005 Nowhere to run and nowhere to hide: response of endemic Mt. Graham red squirrels to catastrophic forest damage. *Biol. Conserv.* **126**, 491–498. (doi:10.1016/j.biocon.2005.06.028)
31. O'Connor CD, Falk DA, Lynch AM, Swetnam TW. 2014 Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient in the Pinaleno Mountains, Arizona, USA. *For. Ecol. Manage.* **329**, 264–278. (doi:10.1016/j.foreco.2014.06.032)
32. Zugmeyer CA, Koprowski JL. 2009 Habitat selection is unaltered after severe insect infestation: concerns for forest-dependent species. *J. Mammal.* **90**, 175–182. (doi:10.1644/07-MAMM-A-399.1)
33. Zugmeyer CA, Koprowski JL. 2009 Severely insect-damaged forest: a temporary trap for red squirrels? *For. Ecol. Manage.* **257**, 464–470. (doi:10.1016/j.foreco.2008.09.020)
34. Smith AA, Mannan RW. 1994 Distinguishing characteristics of Mount Graham red squirrel midden sites. *J. Wildl. Manage.* **58**, 437–445. (doi:10.2307/3809314)
35. Koprowski JL, King SRB, Merrick MJ. 2008 Expanded home ranges in a peripheral population: space use by endangered Mt. Graham red squirrels. *Endanger. Species Res.* **4**, 227–232. (doi:10.3354/esr00026)
36. Koprowski JL. 2002 Handling tree squirrels with a safe and efficient restraint. *Wildl. Soc. Bull.* **30**, 101–103.
37. Larsen KW, Boutin S. 1994 Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. *Ecology* **75**, 214–223. (doi:10.2307/1939395)
38. Lande R. 1996 Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* **76**, 5–13. (doi:10.2307/3545743)
39. Laes D *et al.* 2009 *Mapping vegetation structure in the Pinaleno Mountains using lidar*. RSAC-0118-RPT1, p. 84. U.S. Department of Agriculture, Forest Service, Remote Sensing Applications Center; Salt Lake City, USA.
40. Merrick MJ, Koprowski JL. 2016 Sex-biased natal dispersal at the range periphery: the role of personality, resources, and maternal condition. *Ecol. Evol.*
41. Kreighbaum ME, Van Pelt WE. 1996 Mount Graham red squirrel juvenile dispersal telemetry study, Arizona Game and Fish Department Technical Report **89**, 1–24.
42. Wecker SC. 1963 The role of early experience in habitat selection by the prairie deer mouse, *Peromyscus maniculatus bairdi*. *Ecol. Monogr.* **33**, 307–325. (doi:10.2307/1950749)
43. Remeš V. 2000 How can maladaptive habitat choice generate source–sink population dynamics? *Oikos* **91**, 579–582. (doi:10.1034/j.1600-0706.2000.910320.x)
44. Sih A. 2013 Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Anim. Behav.* **85**, 1077–1088. (doi:10.1016/j.anbehav.2013.02.017)
45. Chalfoun AD, Schmidt KA. 2012 Adaptive breeding-habitat selection: is it for the birds? *Auk* **129**, 589–599. (doi:10.1525/auk.2012.129.4.589)
46. Yoder JM, Marschall EA, Swanson DA. 2004 The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behav. Ecol.* **15**, 469–476. (doi:10.1093/beheco/arih037)
47. Kemink KM, Kesler DC. 2013 Using movement ecology to inform translocation efforts: a case study with an endangered lekking bird species. *Anim. Conserv.* **16**, 449–457. (doi:10.1111/acv.12015)