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Loss of genetic diversity, recovery and allele surfing in a colonizing parasite, *Geomydoecus aurei*

James W. Demastes[1] | David J. Hafner[2] | Mark S. Hafner[3] | Jessica E. Light[4] | Theresa A. Spradling[1]

[1]Department of Biology, University of Northern Iowa, Cedar Falls, Iowa

[2]Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico

[3]Museum of Natural Science and Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana

[4]Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas

Correspondence
James W. Demastes, Department of Biology, University of Northern Iowa, Cedar Falls, IA.
Email: jim.demastes@uni.edu

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Abstract

Understanding the genetic consequences of changes in species distributions has wide-ranging implications for predicting future outcomes of climate change, for protecting threatened or endangered populations and for understanding the history that has led to current genetic patterns within species. Herein, we examine the genetic consequences of range expansion over a 25-year period in a parasite (*Geomydoecus aurei*) that is in the process of expanding its geographic range via invasion of a novel host. By sampling the genetics of 1,935 *G. aurei* lice taken from 64 host individuals collected over this time period using 12 microsatellite markers, we test hypotheses concerning linear spatial expansion, genetic recovery time and allele surfing. We find evidence of decreasing allelic richness (AR) with increasing distance from the source population, supporting a linear, stepping stone model of spatial expansion that emphasizes the effects of repeated bottleneck events during colonization. We provide evidence of post-bottleneck genetic recovery, with average AR of infrapopulations increasing about 30% over the 225-generation span of time observed directly in this study. Our estimates of recovery rate suggest, however, that recovery has plateaued and that this population may not reach genetic diversity levels of the source population without further immigration from the source population. Finally, we employ a grid-based sampling scheme in the region of ongoing population expansion and provide empirical evidence for the power of allele surfing to impart genetic structure on a population, even under conditions of selective neutrality and in a place that lacks strong barriers to gene flow.

KEYWORDS
allele surfing, diversity, expanding population, parasite, population bottleneck

1 | INTRODUCTION

Expansion of the geographic range of a species is a common biological phenomenon, an essential element of the history of every species at some point, yet our understanding of the genetic consequences of range expansion is relatively recent and still developing. The genetic patterns that result from range expansion, however, have wide-ranging implications in biology. For example, given the importance of ongoing climate-driven range shifts in species distributions (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011), it will be important to understand genetic diversity and fitness in expanding populations (Bosshard et al., 2017; Pauls, Nowak, Bálint, & Pfenninger, 2013; Peischl et al., 2018). Similarly, the effect of changing geographic distribution on genetic diversity and its structure is an integral component of the field of biogeography (Waters, Fraser, & Hewitt, 2013) and an important aspect of the global ecological problem of invasive

species (Bock et al., 2015). Finally, genetic consequences of range expansion can be important to systematic studies, because recently established genetic structure of expanding populations may mislead efforts to determine population divergence and complicate efforts to delimit species (Streicher et al., 2016).

Predictions based on simulations of expanding populations have established genetic drift as a potent force in geographically expanding populations because the expansion process itself results from a series of founder events (population bottlenecks) moving through geography (Excoffier & Ray, 2008). As a result of genetic drift, expanding populations are expected to produce a signature of decreasing genetic diversity with increasing geographic distance from the source population (e.g., Austerlitz, Jung-Muller, Godelle, & Gouyon, 1997; Cwynar & MacDonald, 1987; Graciá et al., 2013; Hewitt, 1996; Mayr, 1942; Slatkin & Excoffier, 2012; White, Perkins, Heckel, & Searle, 2013), but this pattern is influenced by the rate of population growth at the colonization front (Nei, Maruyama, & Chakraborty, 1975; Roques, Garnier, Hamel, & Klein, 2012). Importantly, modelling indicates that the spatial patterns of genetic variation imposed by founder events can persist for hundreds or thousands of generations (Ibrahim, Nichols, & Hewitt, 1996).

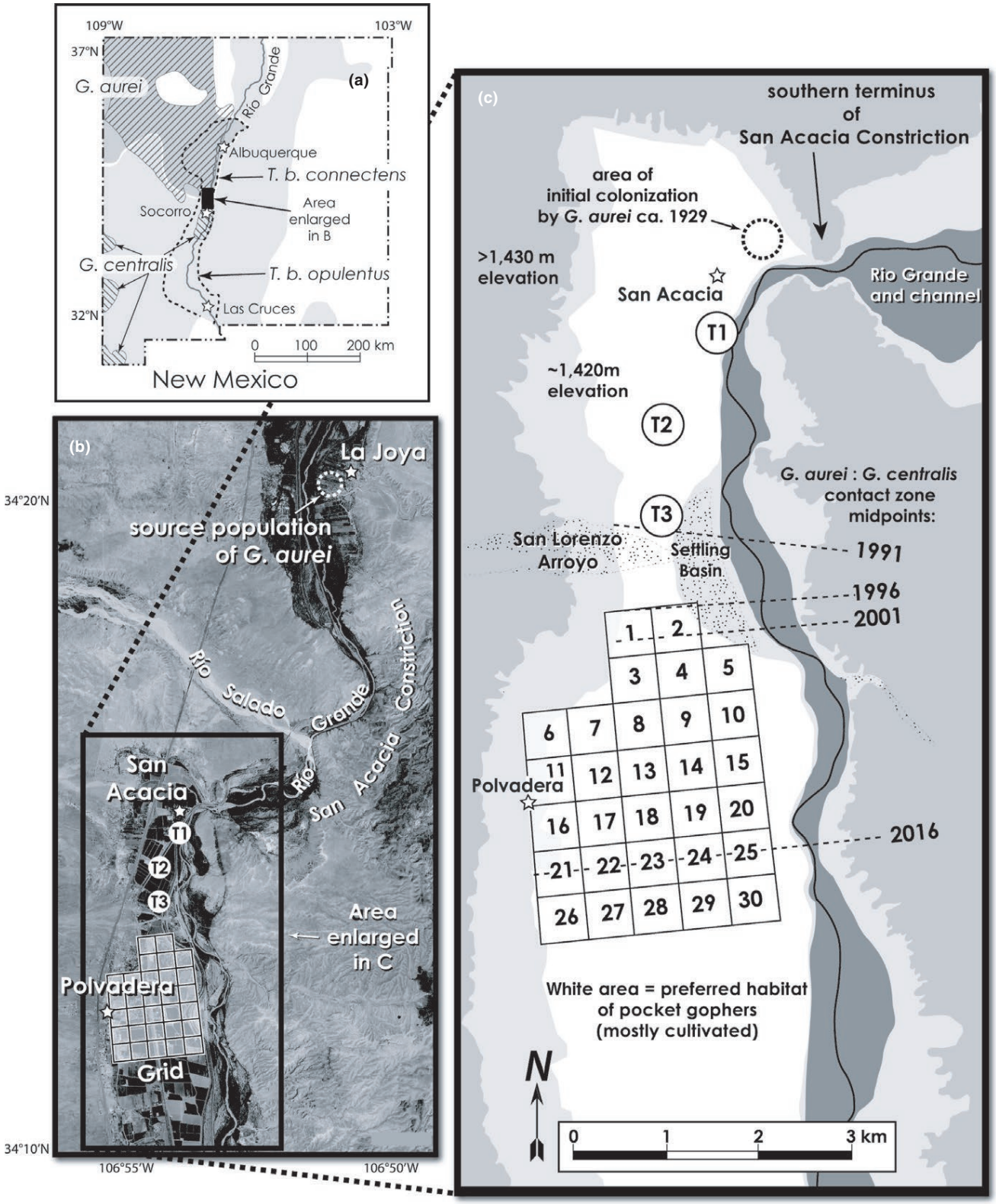
The concept of "allele surfing" (Edmonds, Lillie, & Cavalli-Sforza, 2004; Klopfstein, Currat, & Excoffier, 2006) has emerged as having key explanatory power in modelled populations experiencing geographic range expansion, and the phenomenon has been observed both in cultured bacteria (e.g., Fusco, Gralka, Kayser, Anderson, & Hallatschek, 2016; Gralka et al., 2016; Hallatschek, Hersen, Ramanathan, & Nelson, 2007) and in eukaryotes in their natural environments (Becheler et al., 2016; François et al., 2010; Graciá et al., 2013; Peischl, Dupanloup, Bosshard, & Excoffier, 2016; Pierce et al., 2014; Streicher et al., 2016). Surfing allows rare alleles in a population to reach high frequency through repeated founder events and to become more widespread at the leading edge of population expansion (sometimes referred to as the wave front), where population density is especially low (Excoffier & Ray, 2008). The expansion process can result in a clinal distribution of allele frequencies along the axis of expansion (Excoffier, Foll, & Petit, 2009), and because surfing is stochastic and can occur at multiple points along an advancing wave of population expansion, sectors of low diversity are predicted to form that are each genetically differentiated from neighbouring sectors if migration among demes is somewhat restricted (Excoffier & Ray, 2008). With enough allele surfing, a pattern of genetic differentiation emerges in simulated expanding populations, yielding apparent sectors of the population that run parallel with the axis of population expansion, a pattern that is detectable in axis 1 of principal components analysis (François et al., 2010). Genetic differentiation in expanding populations is compounded when a partial geographic barrier to gene flow allows different alleles to surf on opposite sides of the barrier. And if migration across the barrier is restricted, the degree of genetic differentiation across the barrier is expected to increase the longer surfing along the barrier continues (Novembre & Di Rienzo, 2009; Peischl et al., 2016, pp. 54–55, Figures 1c and 2).

Over the course of 25 years (1990–2016), we have periodically monitored the ongoing geographic range expansion of a species of ectoparasitic chewing louse (*Geomydoecus aurei*; Insecta: Phthiraptera) as it colonizes a novel pocket gopher host (Demastes, 1990, 1996; Demastes, Hafner, Hafner, & Spradling, 1998; Hafner, Hafner, Spradling, Light, & Demastes, 2018; Hafner et al., 1998). This louse species normally is found on the pocket gopher, *Thomomys bottae connectens*, a subspecies that meets and hybridizes to a limited extent with another pocket gopher subspecies, *T. bottae opulentus*, at a physiographic constriction in the Rio Grande Valley in central New Mexico, USA (Hafner et al., 2018; Smith, Patton, Hafner, & Hafner, 1983). This habitat constriction, which we refer to as the San Acacia constriction, appears to have held the pocket gopher hybrid zone in place over a period of decades while the chewing louse, *G. aurei*, has advanced southward, colonizing the southern subspecies of pocket gopher (*T. b. opulentus*) south of the San Acacia constriction (Figure 1a,b; Hafner et al., 1998; Hafner et al., 2018). This host switch is surprising given the host specificity that chewing lice normally show (but see Reed & Hafner, 1997 for other exceptions).

The louse, *G. aurei*, has expanded its range in a southerly direction beginning at an initial colonization site just south of the San Acacia constriction (Figure 1c) and moving southward at what has been a relatively steady rate of 150 metres per year (m/year) over a documented 25-year period (Hafner et al., 2018). In the process of range expansion, *G. aurei* has steadily displaced a congener, *G. centralis*, from the area (Hafner et al., 2018). These lice belong to different phylogenetic groups (Price & Hellenthal, 1981) and show no evidence of hybridization (Demastes, 1990). Thus, it seems that *G. aurei* has a competitive advantage allowing it to displace *G. centralis* in much the same manner as invasive species displace native ones, although the nature of this advantage has not yet been determined. Because *G. aurei* is expanding its range by switching to a new host, this species may serve as an especially consequential model for understanding genetic patterns in expanding populations, given the major medical importance of host shifts or switches by parasites (e.g., Faria et al., 2014; Taylor, Latham, & Mark, 2001).

FIGURE 1 Maps of study site. (a) Species distribution of the lice, *Geomydoecus aurei* and *G. centralis*, and hosts, *Thomomys bottae connectens* and *T. b. opulentus*, in New Mexico with study area shown in black square on Rio Grande. (b) San Acacia constriction region of the Rio Grande Valley; La Joya is part of the historical distribution of *G. aurei* north of the constriction and site of our sampling for a core population. Sampling south of the constriction represents the zone of population expansion for *G. aurei*, which was compared to the core population for assessment of the genetic effects of linear spatial expansion. (c) White shading indicates preferred habitat for pocket gophers (in the irrigated Rio Grande Valley); arid surrounding regions support few pocket gophers. Site T3 was sampled at four times to test for recovery of genetic diversity. Grid cells (numbered) were positioned for sampling such that they would be near the limit of population expansion while remaining in an area with enough population density to allow analysis of allele surfing

Here, we test three hypotheses relating to geographic range expansion using genetic analysis of historical samples of *G. aurei* (1990–1992, 1996, 2001) along with recent (2016) samples: (a) The linear model of spatial expansion (Austerlitz et al., 1997) predicts that expansion-zone populations will show less genetic diversity than core populations and that genetic diversity will decrease with distance from the initial colonization site. We test this hypothesis by comparing the genetic structure of leading-edge populations to those at the core of the species distribution over two time periods. Evidence contrary to the above prediction would reject the linear



model hypothesis as it pertains to this system and would support the potential influence of an Allee effect, which can preserve diversity at the leading edge of expansion (Roques et al., 2012), or of leapfrog dispersal rather than stepping stone dispersal (Becheler et al., 2016). (b) Simulations by Ibrahim et al. (1996) predict that formerly bottlenecked populations at the leading edge of range expansion will be slow to recover from bottleneck events and retain evidence of the event hundreds of generations after initial colonization. We test the *recovery-time model* by comparing the genetic diversity of populations at three different stages of recovery after our initial sampling. Evidence of rapid recovery (or no recovery) of genetic diversity at this zone would reject Ibrahim et al.'s (1996) hypothesis. (c) The *allele-surfing model* (François et al., 2010) predicts that expanding populations will show greater genetic variation along an axis perpendicular to the axis of expansion than along an axis parallel to it. We test this hypothesis by sampling a plot of evenly spaced samples (a grid) from the zone of population expansion.

In this study, all louse individuals of the same species on a single host (i.e., an "infrapopulation," Esch, Gibbons, & Bourque, 1975) are treated as an individual population unit or deme in our analyses. This approach is justified because *Geomydoecus* lice are obligate parasites of pocket gophers that have not been reported on other species of mammals, and louse transmission among individual hosts is greatly restricted by specializations and behaviours of both lice and their hosts (reviewed in Hafner, Demastes, Spradling, & Reed, 2003). Genetic data from the chewing lice of pocket gophers at a single locality indicate restricted dispersal from one host to another, reinforcing the importance of the infrapopulation as a fundamental population unit for these animals (Harper, Spradling, Demastes, & Calhoun, 2015; Nadler, Hafner, Hafner, & Hafner, 1990; Nessner, Andersen, Renshaw, Giresi, & Light, 2014). To test our three hypotheses concerning the genetics of range expansion, we sampled the genetics of 1,935 *G. aurei* louse individuals from 64 host individuals (i.e., 64 infrapopulations) using 12 microsatellite markers. For hypotheses concerning linear spatial expansion, sampling included individuals from the core of the species distribution north of the San Acacia constriction, where *G. aurei* genetic diversity is presumably at normal levels, for comparison with samples of lice in the zone of population expansion south of the constriction. To test recovery time, genetic diversity of infrapopulations from a single site was assessed for four different time periods (1991, 1996, 2001 and 2016) reflecting 5, 10 and 25 years for genetic recovery following the initial population sample. Given an estimated generation time of chewing lice near 40 days (Rust, 1974), these time points represent about 45, 90 and 225 louse generations for genetic recovery. Finally, in 2016, a 30-cell grid formed by five north–south transects and seven east–west transects encompassing the current zone of population expansion was sampled to allow a detailed analysis of genetic variation over geography for assessment of potential allele surfing (Figure 1). We should note that this area is typical of New Mexico flood-irrigation agriculture with the associated unpaved access roads and diversion canals. Several of these otherwise minor potential impediments to gopher dispersal converge to form a multilayered feature comprising two drainage canals, an elevated and rocky railroad bed, and a paved road running north–south through the central column of the grid, all within a narrow (100 m wide) band. This presents the only obvious potential restriction to gopher dispersal in our study area, a four-tier, partial reflective boundary (sensu Burton & Travis, 2008). Thus, the geographic features of our study site are similar to those depicted by Peischl et al. (2016; Figures 1c and 2) with a potential partial barrier to gene flow parallel to the expansion axis that would be expected to accentuate the effects of divergent surfing events on opposite sides of the partial barrier by promoting southward gene flow in the expanding population over east–west gene flow. Thus, this system presents a unique opportunity to study the effect of a documented, ongoing population expansion on genetic diversity and genetic structure in hundreds of individuals over hundreds of generations.

2 | METHODS

2.1 | Sampling and laboratory methods

The New Mexico Department of Game and Fish approved collection of pocket gopher (*Thomomys bottae*) specimens over all time periods, and procedures followed guidelines set by the University of Northern Iowa Institutional Animal Care and Use Committee and the American Society of Mammalogists (Sikes & the Animal Care and Use Committee of the American Society of Mammalogists, 2016). Lice from each host individual were placed in labelled Nunc CryoTube vials (Nalge Nunc International, Denmark) and stored on dry ice or in liquid nitrogen until returned to the laboratory, where they were stored at −80°C. Samples from 1990 to 1992 and from 1996 were collected for studies reported by Hafner et al. (1998). These samples have been stored continuously at −80°C since the time of their collection. Four infrapopulations collected in 2001 as part of unpublished work verifying the continued southward progression of *G. aurei* range expansion were included for comparisons of genetic diversity over time as they also met the requirements of being near the zone of range expansion as it existed in 2001 and having 30 or more individuals per infrapopulation available for DNA extraction (Hale, Burg, & Steeves, 2012). For analyses of the genetic effects of linear spatial expansion and of recovery time, the sites of population expansion examined for *G. aurei* in 1991, 1996 and 2001 were resampled in 2016, as was the core population of La Joya, New Mexico (Figure 1, Table 1).

Details of our efforts to locate the 2016 position of the front of the zone of *G. aurei* population expansion are reported in Hafner et al., 2018). From these data, it was determined that the southern edge of the zone of *G. aurei* population expansion lies near 34.1938°N latitude. In preparation for sample collection, a sampling grid was devised and overlaid on maps depicting the Río Grande floodplain (preferred pocket gopher habitat), with the southern row of the grid centred at 34.1938°N. Thirty cells were spaced to cover the maximum available habitat in the area of *G. aurei* population expansion while keeping grid centres at a distance of 500 m, a distance greater

than the gopher average annual dispersal distance of 400 m/year estimated for this pocket gopher species in this region of New Mexico (Hafner et al., 1998). Trappers collected as near the centre of each grid as feasible, and GPS coordinates were recorded for each specimen collected at the time of capture. Where multiple specimens were collected in a single grid cell, louse infrapopulations closest to the grid centre were selected for genetic analysis.

Extraction of DNA from individual lice was carried out as described by Harper et al. (2015). DNA from each individual was amplified in a series of 4–5 multiplex PCRs using primers for 12 microsatellite loci (Light, Harper, Johnson, Demastes, & Spradling, 2018). These 12 markers were demonstrated to yield high-quality genotypes with locus-specific genotyping error rates near zero, no evidence of genotypic disequilibrium and no evidence of null alleles in *G. aurei* from La Joya, New Mexico (Light et al., 2018). Amplification products were sent to the Iowa State University DNA Facility for analysis on an Applied Biosystems 3730 DNA Analyzer. Output electropherogram files were inspected visually, edited manually and scored at least twice per sample for verification purposes using GENEMARKER software (version 1.90; SoftGenetics, State College, PA, USA). In total, 1,935 lice representing 64 infrapopulations of lice were fully genotyped for 12 loci, with no missing data. Numbers of *G. aurei* genotyped per infrapopulation ranged from 21 to 38 individuals (mean = 30.2, Table 1). Data from 13 of these infrapopulations also appear in Light et al. (2018). The software CONVERT (version 1.31; Glaubitz, 2004) was used to reformat all data files for use in additional genetic analysis programs.

2.2 | Analysis of linear spatial expansion

For comparisons of genetic diversity north versus south of the San Acacia constriction, allelic richness (AR) calculated with rarefaction, observed heterozygosity (H_O) and expected heterozygosity (H_E) were determined using the DIVERSITY package (Keenan, McGinnity, Cross, Crozier, & Prodöhl, 2013) for R (version 3.3.3, R Core Team, 2014) implemented using RSTUDIO version 1.0.136 (RStudio Team, 2016). Rarefaction values in DIVERSITY were calculated using the method of Kalinowski (2004; K. Keenan, personal communication). For consistency in AR estimates from one analysis to another, we used all 64 available infrapopulations of lice in a single analysis of AR. Inbreeding coefficients (F_{IS}) were calculated using the DIVERSITY package. AR scores were mapped to geography using the R-package GGMAP (version 2.6.1, Kahle & Wickham, 2013).

Comparisons of genetic diversity between core and expansion-zone populations were one-tailed given that genetic diversity was expected to be higher in core infrapopulations than in those of the expansion zone. Mean genetic diversities for groups of infrapopulations collected north of the San Acacia constriction and south of the constriction were compared using one-tailed, two-sample *t* tests assuming unequal variances in Excel (© 2017, Microsoft). In the case of this *t* test and others, the spacing of louse infrapopulation samples greater than one average annual dispersal distance for the hosts (Hafner et al., 1998) helps assure the assumption of independent observations was not violated.

For linear spatial analysis within the zone of population expansion, infrapopulations collected south of the San Acacia constriction were assigned a "meters along transect" value (Table 1) using methods and values calculated by Hafner et al. (2018). In short, this value indicates the position of an infrapopulation on our north–south sampling transect with the location of initial colonization by *G. aurei* south of the San Acacia constriction designated as the zero point, or start, for transect measurements (Figure 1c). The transect was labelled in 200 m increments that ran, for the samples included in this study, 7.4 km southward. Excel (© 2017, Microsoft) was used for regression analyses for tests of a possible relationship between distance from the colonization site and either genetic diversity or inbreeding coefficient.

2.3 | Analysis of recovery time

To assess potential changes in genetic diversity (AR) over time, we compared AR and H_E of samples collected at a single site (T3 of Figure 1 and Table 1) at four different times. These infrapopulations were collected no more than 600 m from one another. Excel (© 2017, Microsoft) was used for regression analysis of AR over time at this single site. Where linear regression analyses resulted in a distribution of standardized residuals that suggested non-linear relationships between variables, data were further explored using a generalized additive model for smoothing in MGCV version 1.8-22 (Wood, 2011) as described by Jones and Almond (1992). Multiple runs at a variety of *K* values were performed to determine the model that explained the greatest per cent deviance. Results were visualized using GGPLOT2 (version 2.2.1, Wickham, 2009). Mean AR ($\overline{AR}$) for infrapopulations collected at different times was compared using one-way ANOVA followed by Tukey's HSD (honest significant difference) test in the AGRICOLAE package (version 1.2-8) for R. Tests were one-tailed because genetic diversity was expected to be higher after more time for recovery.

2.4 | Analysis of allele surfing

Allele surfing predicts genetic structure among infrapopulations that differentiates them more perpendicular to the axis of expansion (in this case on an east–west axis) than along a path of colonization parallel with the axis of expansion (i.e., north–south; François et al., 2010). To test this prediction, we used 26 infrapopulations collected in 2016 south of the San Acacia constriction, which included a grid-style sampling scheme, and eight infrapopulations from a well-sampled region directly north of the grid (grid cells and sites T1–T3 of Figure 1c). The potential presence of isolation by distance (IBD) in lice was investigated using a Mantel test (Mantel, 1967), as implemented in the ADEGENET R-package, for the 26 grid infrapopulations of lice. For the Mantel test, Edwards' distance was calculated (Edwards, 1971) for louse microsatellite data, and Euclidean distances were

TABLE 1 Infrapopulations of *G. aurei* sampled with year of collection, host specimen collector number, genetic diversity measures, sample size of infrapopulation, site name, analyses performed and meters along the transect indicating distance from the site of population colonization, museum accession number for the host† and collection coordinates. Site names correspond to Figure 1, where "G" indicates a numbered grid site, and analysis names correspond with methods and results. The four grid sites listed as having 0 lice had only, or predominantly, G. centralis lice there, with few or no G. aurei for genetic analysis; the few G. aurei samples recovered from these sites were not included in population analyses

Year	Host Specimen	Allelic Richness	H_O	H_E	F_{IS}	#Lice	Site name
1992	DLR 257	3.72	0.56	0.54	−0.05	31	0
1992	TSD 435	4.25	0.54	0.55	0.02	29	0
1992	TSD 437	3.96	0.55	0.53	−0.03	28	0
1992	TSD 439	4.19	0.52	0.55	0.07	29	0
1990	JWD 70	3.28	0.48	0.52	0.06	31	T1
1991	MSH 1437	3.02	0.43	0.42	−0.04	31	T1–T2
1991	DJH 3354	3.40	0.48	0.51	0.03	31	T2
1991	MSH 1428	2.90	0.50	0.47	−0.06	29	T2
1991	MSH 1425	3.43	0.52	0.49	−0.06	32	T2
1991	MSH 1423	3.21	0.46	0.46	−0.02	32	T2
1991	DJH 3340	2.70	0.50	0.49	−0.03	27	T3
1991	DJH 3348	2.67	0.47	0.46	0.06	31	T3
1996	MSH 1472	3.59	0.56	0.55	−0.01	32	T2
1996	JWD 282	3.32	0.56	0.54	−0.02	31	T3
1996	JWD 283	3.19	0.43	0.46	0.05	32	T3
1996	TAS 609	3.36	0.50	0.49	−0.03	32	T3
1996	MSH 1486	3.33	0.52	0.50	−0.02	31	T3
2001	DJH 4670	3.25	0.58	0.53	−0.08	30	T3
2001	MSH 1543	3.65	0.52	0.53	−0.01	31	T3
2001	DJH 4659	3.48	0.53	0.53	0.01	31	T3
2001	DJH 4673	3.36	0.52	0.51	−0.02	31	G2
2011	TAS 758	4.12	0.59	0.55	−0.08	31	0
2011	TAS 760	4.00	0.62	0.59	−0.05	27	0
2011	TAS 761	4.40	0.60	0.59	−0.02	29	0
2011	TAS 762	4.07	0.54	0.51	−0.05	32	0
2016	TAS 822	3.84	0.55	0.54	0.00	31	0
2016	TAS 825	4.12	0.55	0.54	−0.01	38	0
2016	TAS 826	4.21	0.60	0.57	−0.04	27	0
2016	TAS 823	4.09	0.56	0.56	−0.02	28	0
2016	TAS 821	4.24	0.57	0.58	0.03	30	0
2016	TAS 828	3.69	0.53	0.52	−0.02	34	T1
2016	TAS 833	3.61	0.54	0.56	0.03	30	T2
2016	TAS 841	3.37	0.49	0.51	0.05	32	T2
2016	TAS 838	3.31	0.49	0.49	0.00	30	T2
2016	TAS 840	3.51	0.55	0.53	−0.06	28	T2
2016	TAS 813	3.42	0.46	0.52	0.12	27	T3
2016	TAS 818	3.41	0.54	0.52	−0.04	35	T3
2016	TAS 820	3.58	0.57	0.56	−0.03	25	T3
2016	TAS 810	3.63	0.56	0.52	−0.09	34	G1
2016	TAS 845	3.40	0.51	0.49	−0.05	32	G2

Analyses	Distance from colonization site (m)	Voucher information	Latitude	Longitude
La Joya (core)	–	LSUMZ 33915	34.331000	−106.846667
La Joya (core)	–	LSUMZ 30743	34.331000	−106.846667
La Joya (core)	–	LSUMZ 30744	34.331000	−106.846667
La Joya (core)	–	LSUMZ 30785	34.331000	−106.846667
Expansion	1,600	MSB 287571	34.246803	−106.901649
Expansion	2,200	LSUMZ 30865	34.242122	−106.901313
Expansion	2,800	LSUMZ 30714	34.235606	−106.910038
Expansion	2,800	LSUMZ 30904	34.237735	−106.902373
Expansion	3,000	LSUMZ 30788	34.232831	−106.904328
Expansion	3,200	LSUMZ 30929	34.232152	−106.904635
Expansion, recovery	3,200	LSUMZ 30862	34.232010	−106.912285
Expansion, recovery	3,400	LSUMZ 30924	34.231346	−106.911967
Expansion	3,000	LSUMZ 35985	34.234689	−106.903483
Expansion, recovery	3,200	LSUMZ 36007	34.233925	−106.911223
Expansion, recovery	3,600	LSUMZ 36016	34.229246	−106.909582
Expansion, recovery	3,600	LSUMZ 35994	34.229066	−106.908368
Expansion, recovery	3,800	LSUMZ 35997	34.228716	−106.911226
Expansion, recovery	3,400	MSB 287945	34.233452	−106.911669
Expansion, recovery	3,400	MSB 287630	34.232004	−106.912126
Expansion, recovery	3,800	MSB 287628	34.228679	−106.910219
Expansion	4,200	MSB 287948	34.223303	−106.908841
La Joya (core)	–	TCWC 64971	34.332361	−106.846940
La Joya (core)	–	TCWC 64973	34.331889	−106.847060
La Joya (core)	–	TCWC 64974	34.331750	−106.848080
La Joya (core)	–	TCWC 64975	34.333611	−106.847780
La Joya (core)	–	TCWC 64298	34.330470	−106.852580
La Joya (core)	–	TCWC 64301	34.332310	−106.847810
La Joya (core)	–	TCWC 64302	34.332160	−106.848680
La Joya (core)	–	TCWC 64299	34.331700	−106.846750
La Joya (core)	–	TCWC 64297	34.330720	−106.851430
Expansion, linear	1600	TCWC 64304	34.246810	−106.901540
Expansion, linear	2,400	TCWC 64309	34.239180	−106.907820
Expansion, linear	2,800	TCWC 64317	34.237050	−106.908450
Expansion, linear	2,800	TCWC 64314	34.236710	−106.908930
Expansion, linear	3,200	TCWC 64316	34.232800	−106.905650
Expansion, linear, recovery	3,400	TCWC 64289	34.23004	−106.909030
Expansion, linear, recovery	3,400	TCWC 64294	34.22957	−106.909830
Expansion, linear, recovery	3,400	TCWC 64296	34.22934	−106.909120
Expansion, linear, grid	4,400	TCWC 64286	34.220710	−106.909530
Expansion, grid	4,600	TCWC 64321	34.220080	−106.904540

(Continues)

TABLE 1 (Continued)

Year	Host Specimen	Allelic Richness	H_O	H_E	F_{IS}	#Lice	Site name
2016	TAS 865	3.39	0.54	0.52	−0.04	28	G3
2016	TAS 849	3.49	0.48	0.51	0.07	32	G4
2016	TAS 844	3.36	0.45	0.49	0.10	32	G5
2016	TAS 852	3.10	0.51	0.48	−0.05	31	G6
2016	TAS 856	3.07	0.49	0.48	0.00	32	G7
2016	TAS 784	3.35	0.52	0.49	−0.06	28	G8
2016	TAS 863	3.07	0.48	0.46	−0.07	30	G9
2016	TAS 860	3.47	0.51	0.51	0.00	31	G10
2016	TAS 878	3.07	0.47	0.46	−0.05	32	G11
2016	TAS 857	2.98	0.51	0.48	−0.05	32	G12
2016	TAS 866	3.13	0.47	0.49	0.04	31	G13
2016	TAS 874	3.36	0.53	0.53	−0.01	32	G14
2016	TAS 877	3.13	0.50	0.47	−0.04	31	G15
						0	G16
2016	TAS 869	2.89	0.49	0.50	0.01	29	G17
2016	TAS 789	3.17	0.49	0.48	−0.02	30	G18
2016	TAS 888	3.32	0.55	0.52	−0.07	31	G19
2016	TAS 884	3.33	0.47	0.47	−0.04	32	G20
						0	G21
2016	TAS 901	3.05	0.47	0.49	0.05	27	G22
2016	TAS 868	2.97	0.52	0.48	−0.07	31	G23
2016	TAS 909	2.62	0.44	0.42	−0.06	31	G24
2016	TAS 906	3.06	0.51	0.49	−0.03	26	G25
						0	G26
						0	G27
2016	TAS 896	2.51	0.45	0.41	−0.08	22	G28
2016	TAS 916	2.62	0.42	0.40	−0.07	21	G29
2016	TAS 910	3.07	0.48	0.49	−0.01	31	G30

[†]LSUMZ: Louisiana State University Museum of Natural Science; MSB: Museum of Southwestern Biology, University of New Mexico; TCWC: Biodiversity Research and Teaching Collections at Texas A&M University.

calculated for geographic coordinates. Probabilities were calculated based on 1,000 Monte Carlo simulations.

Because these analyses include closely related infrapopulations and complex allelic data, we used multivariate analyses to more efficiently detect genetic patterns relative to spatial information (Jombart, Devillard, Dufour, & Pontier, 2008; Jombart, Pontier, & Dufour, 2009). A Bayesian cluster method, GENELAND (version 4.0.7, Guillot, Mortier, & Estoup, 2005), was used to investigate population structure in the 34 infrapopulations of lice collected in 2016 from south of San Acacia. This analysis is well suited for detecting reduced gene flow under migration scenarios (Safner, Miller, McRae, Fortin, & Manel, 2011). GENELAND was run using the uncorrelated frequency model for 1×10^6 iterations with a thinning interval of 1,000, and *K* was free to vary. Spatial PCA (sPCA) and Monmonier analysis to detect maximum-difference boundaries in the spatial data (Manni, Guerard, & Heyer, 2004; Monmonier, 1973) were performed using a Delaunay triangulation grid in the R-package ADEGENET (version 2.0.1, Jombart, 2008; Jombart & Ahmed, 2011). For sPCA, Monte Carlo simulation of special weights was used to test the null hypothesis of absence of spatial structure using ADE4 (version 1.7-6, Dray & Dufour, 2007).

To determine whether host population structure has any influence on louse population structure at the scale under consideration in this study, genotypes for four genes were determined for the 39 pocket gophers that hosted louse infrapopulations sampled in 2016 (Table S1, Supporting Information). Mantel analyses were used to compare host differentiation to parasite differentiation and to compare host differentiation to geography (Mantel, 1967); Euclidean distances were used for both geographic coordinates and pocket gopher sequence data. STRUCTURE (version 2.3.4; Falush, Stephens, & Pritchard, 2003; Hubisz, Falush, Falush, Stephens, & Prichard, 2009; Pritchard, Stephens, & Donnelly, 2000), BAPS (version 6.0, Corander, Marttinen, Sirén, & Tang, 2008) and GENELAND (version 4.0.7, Guillot et al., 2005) were used to

Analyses	Distance from colonization site (m)	Voucher information	Latitude	Longitude
Expansion, linear, grid	4,800	TCWC 64341	34.216270	−106.908910
Expansion, grid	4,800	TCWC 64325	34.218170	−106.904500
Expansion, grid	4,800	TCWC 64320	34.217040	−106.897970
Expansion, grid	5,400	TCWC 64328	34.210460	−106.919050
Expansion, grid	5,400	TCWC 64332	34.211400	−106.913570
Expansion, linear, grid	5,400	TCWC 64260	34.211560	−106.909260
Expansion, grid	5,400	TCWC 64339	34.211170	−106.905370
Expansion, grid	5,200	TCWC 64336	34.213470	−106.898410
Expansion, grid	5,800	TCWC 64354	34.207280	−106.919790
Expansion, grid	5,800	TCWC 64333	34.206710	−106.913300
Expansion, linear, grid	5,800	TCWC 64342	34.207080	−106.908580
Expansion, grid	5,800	TCWC 64350	34.208400	−106.902820
Expansion, grid	5,800	TCWC 64353	34.208170	−106.896970
Expansion, grid	6,400	TCWC 64345	34.202410	−106.912740
Expansion, linear, grid	6,400	TCWC 64265	34.202510	−106.907600
Expansion, grid	6,400	TCWC 64364	34.203350	−106.901550
Expansion, grid	6,400	TCWC 64360	34.204540	−106.896520
Expansion, grid	7,000	TCWC 64377	34.198040	−106.913100
Expansion, linear, grid	6,800	TCWC 64344	34.198730	−106.907030
Expansion, grid	7,000	TCWC 64385	34.198320	−106.900700
Expansion, grid	7,200	TCWC 64382	34.197550	−106.895700
Expansion, linear, grid	7,400	TCWC 64372	34.193280	−106.905950
Expansion, grid	7,400	TCWC 64392	34.194370	−106.900570
Expansion, grid	7,400	TCWC 64386	34.193920	−106.896180

examine potential spatial structure within the 34 pocket gophers from south of San Acacia both with and without spatial coordinates being input in the analysis (Supporting Information, Pocket Gopher Methods).

We identified the subset of alleles that might be surfing by comparing allele frequencies in infrapopulations from the north end of our 2016 samples (locality T1–T3) with those at the southern end of our grid. We applied linear regression analysis (Excel © 2017, Microsoft) to those alleles that showed at least 20% increase in frequency at the leading edge of spatial expansion (following the approach of Pereira, Teixeira, & Velo-Antón, 2018). Alleles that showed a significant, positive slope in regression were considered to have surfed. Significance of slope was determined using standard *F* tests and permutation tests as implemented in the LMPERM package (Wheeler, 2010) using the *Prob* option (Anscombe, 1953).

To test whether any of the microsatellite loci used in this study were subject to selection in this geographic region, an F_{ST} outlier test was performed on chewing louse infrapopulations using BAYESCAN 2.1 assuming a conservative prior odds for the neutral model of 10 (Foll & Gaggiotti, 2008). For the Markov chain Monte Carlo algorithm implemented in BAYESCAN, we started with 20 pilot runs of 5,000 iterations with burn-in set to 50,000, followed by 50,000 iterations (thinning interval of 10 and sample size of 5,000). Convergence was confirmed using the R-package CODA (Plummer, Best, Cowles, & Vines, 2006). We used the false discovery rate (FDR) of 0.05 to control for multiple testing (Benjamini & Hochberg, 1995).

3 | RESULTS

3.1 | Ongoing spatial expansion

Geomydoecus aurei population expansion has progressed at a pace of approximately 150 m/year over the last 25 years (Hafner et al.,

2018). Population expansion, however, did not occur at even rates along all sectors of the Rio Grande Valley, as *G. aurei* were present in small numbers or absent in some parts of our sampling grid (Figure 1c). Although the species was present in grid cell 16, it was not present in large enough numbers for genetic analysis, and it was completely absent from grid cells 21, 26 and 27 (i.e., the southwestern corner of the grid). Along the southern edge of our grid, *G. centralis* was the predominant louse, with only one pocket gopher in cell 28 and one in cell 29 bearing sufficient numbers of *G. aurei* for genetic analysis (n = 22 and n = 21, respectively; Table 1). In the other 23 cells of the grid, *G. aurei* dominated the louse community as either the only *Geomydoecus* louse on pocket gophers or outnumbering *G. centralis* by a ratio of >10:1. Thus, *G. aurei* became more difficult to find on pocket gophers nearer the southern end of our grid, as expected for sampling at the front of a southwardly progressing population expansion, and the species' range expansion on the western edge of the valley has lagged about 1 km behind that of mid-valley populations.

3.2 | Effects of linear spatial expansion

3.2.1 | Core versus expansion zone

From the 390 lice sampled in the core of the species distribution in the north at La Joya ("core" in Table 1) and 1,545 lice sampled in the population-expansion zone south of the constriction ("expansion" in Table 1), there were 78 alleles recovered at the 12 loci. Nine alleles were private to the north and only seven alleles private to the south, despite our much more intensive sampling in the south. Allelic richness, which is adjusted for unequal sample sizes, was higher for the pool of all lice from north of the constriction than for the pool of all lice south of the constriction (AR = 5.7 vs. 5.1).

Genetic diversity of individual infrapopulations from the core of the species distribution was higher than for infrapopulations from south of the constriction in the population-expansion zone. When all time periods were included in a single analysis, AR for every infrapopulation of *G. aurei* north of the constriction was higher than that of any infrapopulation from south of it (AR ranged 3.72–4.40 north of the constriction and 2.51–3.69 south of it; Table 1). The resulting difference in mean AR ($\overline{AR}$) was significant (4.1 in the north vs. 3.2 in the south, one-tailed, two-sample t test assuming unequal variances, df = 29, $p < 0.001$). This pattern of significantly higher $\overline{AR}$ in core *G. aurei* infrapopulations than in southern, expansion-zone infrapopulations was evident for both time periods in which sampling occurred both north and south of the San Acacia constriction (1990–1992 and 2016, two-sample t test assuming unequal variances, df = 8, $p < 0.001$ for both time periods). The reduced diversity of infrapopulations from the population-expansion zone south of the constriction versus lice at the core of the species distribution north of the constriction is easily distinguished visually for both 1990–1992 (Figure 2a) and 2016 (Figure 2b).

Another measure of genetic diversity, H_E (Table 1), likewise showed significantly higher diversity in infrapopulations from the core population north of the constriction (mean H_E = 0.55) than in the expanding populations south of the constriction (mean H_E = 0.49; one-tailed, two-sample t test assuming unequal variances, df = 28, $p < 0.001$). Inbreeding (F_{IS}) was near zero for all infrapopulations and not significantly related to geography in any comparison over any time period or in the pooled data.

3.2.2 | Genetic diversity within the expansion zone

South of the San Acacia constriction, where population expansion is ongoing, genetic diversity (AR) decreased with distance from the presumed site of initial colonization (Figure 2b, Table 1). The decrease in genetic diversity over distance from the initial colonization site was significant whether the response variable considered was AR (Figure 3; F = 49.6, $p < 0.001$, R^2 = 0.61) or gene diversity (H_E; F = 27.8, $p < 0.001$, R^2 = 0.46). This relationship remained significant when the analysis was restricted to infrapopulations sampled in a straight line from site T1 through the middle of the grid (samples indicated as "linear" analysis, Table 1); this analysis minimized the impact of any east–west louse population expansion. For these 15 samples, there was a significant reduction in genetic diversity associated with increasing distance from the colonization site, whether diversity was measured as AR or as H_E (AR: F = 22.8, $p < 0.001$, R^2 = 0.64; H_E: F = 17.8, $p < 0.001$, R^2 = 0.57).

As an alternative approach to comparing genetic diversity in infrapopulations from nearer the core of the species distribution with infrapopulations farther away, AR of the northernmost 2016 sample of each north–south grid transect was compared with AR of the southernmost sample of that transect (i.e., G6 vs. G11, G7 vs. G22, G1 vs. G28, G2 vs. G29, G5 vs. G30; Figure 1c). In every comparison, there was higher AR in the northern infrapopulation versus the southern one, together indicating significantly lower diversity farther from the colonization site (one-tailed, two-sample t test assuming unequal variances, df = 8, p = 0.01), a pattern evident on visual inspection of AR (Figure 2b). For the other three time periods sampled, the pattern of lower AR in the sample farther from the colonization site held in all but one comparison (2001). For all time periods combined, the lower AR in samples more distant from the original colonization site was significant (one-tailed, two-sample t test assuming equal variances, df = 9, p = 0.02).

3.3 | Recovery of genetic diversity

Given the apparent loss of genetic diversity in lice in the zone of population expansion relative to the core of the species distribution, a comparison of AR over time was performed to determine whether there was measurable recovery in AR in the zone of population expansion over the 25-year time between our initial sampling and our 2016 sampling. We addressed genetic recovery by considering only infrapopulations from a small geographic area (≤600 m between samples) that was resampled at four points in time (site T3 in Figure 1, "recovery" in Table 1). Sampling included

363 lice: 58 lice from 1991, 126 lice from 1996, 92 lice from 2001 and 87 lice from 2016. We observed an increase in $\overline{AR}$ over most time comparisons until 2016, which showed a modest decrease in $\overline{AR}$ ($\overline{AR}$ = 2.69, 3.29, 3.57, 3.47 for 1991, 1996, 2001 and 2016, respectively). Genetic diversity ($\overline{AR}$) was significantly lower in 1991 infrapopulations compared with all later times (ANOVA, $p \leq 0.03$ for each one-tailed test, Tukey's HSD). Other differences (i.e., 1996 vs. 2001, 1996 vs. 2016 and 2001 vs. 2016) were not significant. The greatest increase in genetic diversity occurred between the initial sampling period and the next sampling period, five years later, amounting to a 22% increase in $\overline{AR}$. The next sampling period, another 5 years later, showed a more modest 10% increase in genetic diversity (32% total increase over the first 10 years or 90 generations). Linear regression results indicated a positive relationship between time for recovery and $\overline{AR}$($F = 6.7$, $R^2 = 0.40$, $p = 0.03$). However, analysis of residuals indicated a non-linear relationship between these variables, suggesting the utility of a generalized additive model. This analysis (Figure 4) indicated an initially steep rise in $\overline{AR}$ soon after population establishment that was followed by a plateau during which there was little change in $\overline{AR}$ over time ($F = 19.7$, $R^2 = 0.84$, $p < 0.001$). Regression analysis also showed a significant increase in H_E over time ($F = 6.2$, $R^2 = 0.38$, $p = 0.03$).

In the area of louse population expansion south of the San Acacia constriction, we recovered seven private alleles at the 12 loci examined. Each of these could potentially represent a new mutation not present in the core of the species distribution, but it seems more likely that detection of these alleles was facilitated by our more intense sampling of populations in the south than in the north (1,545 vs. 390 lice, respectively). Still, it could be of interest to know how many new alleles could be expected to appear in the zone of population expansion over the time period examined. This prospect relies on our ability to estimate a mutation rate for microsatellites, which is not uniform among species (Ellegren, 2004). Mutation rate also exhibits a wide range of values even within a species for microsatellite loci, ranging from 10^{-6} to 10^{-2} mutations per locus per generation, with actual mutation rate depending on allele-specific factors such as motif size, length, sequence composition and presence of nearby repeat motifs (Eckert & Hile, 2009). Using these estimates of mutation rate as a crude guide, the mutational process could produce anywhere from 0.0002 to 2 mutations per locus (i.e., anywhere from zero to 24 new alleles for all 12 loci examined).

3.4 | Allele surfing

Because a pattern of isolation by distance was present in the louse infrapopulations as indicated by the significant association between genetic distance and geographic distance for the 26 grid infrapopulations (Mantel test, $r = 0.35$, $p = 0.001$), we used spatially explicit analyses of genetic structure (Geneland and sPCA; Safner et al., 2011; Meirmans, 2012). Bayesian clustering analysis (Geneland) identified three genetic groups within the 34 infrapopulations of lice sampled south of San Acacia in 2016. These three optimum groups corresponded with a largely northern cluster of infrapopulations, a western group and an eastern group (Figure 5a). The boundary between eastern and western lice is near, but not perfectly coincident with, the four-tier partial barrier to gene flow (Figure 5a). Spatial analysis of genetic variance resulted in one clearly distinct principal component (Figure S1, Supporting Information, PC 1 = 17.7% of total variance), which indicated two distinct genetic groups (Figure 5b). Monmonier analysis detected a boundary between these eastern and western infrapopulations (Figure 5b).

Analysis of host genetics yielded 30 alleles for population analysis (Table S1). South of the San Acacia constriction, where louse infrapopulations showed strong evidence of population structure, pocket gophers did not show population structure in STRUCTURE (Figure S2), BAPS or GENELAND analyses (Supporting Information, Pocket Gopher Results). Mantel analysis of host-individual genetic distance versus parasite infrapopulation genetic distance also did not indicate any significant relationship ($p = 0.529$) between host and parasite genetic distance.

All analyses of genetic structure indicated a pattern of differentiation between louse infrapopulations on the eastern half of the grid and those on the western half, and surfing may have propelled a different set of alleles southward in the two regions. Thus, we conducted analyses of allele frequency increase over these two subsets of the geographic space, with groups defined as northern, western or eastern as indicated by the results of Geneland analysis (Figure 5a). Six of 12 loci examined had an allele that increased significantly in frequency in a clinal pattern from north to south (i.e., in the direction of spatial expansion) over all or a portion of the geographic space considered (Figure S3). Allele 221 of locus 4863 increased significantly (surfed) on both the eastern and the western sides of the geographic space (Figure S3a,b). The other five alleles showed a clinal pattern of allele frequency increase only on one side of the grid; for example, allele 247 of locus 4911 surfed only on the western side of the geographic space examined (Figure S3c), but not on the eastern side (Figure S3d). Four additional loci (Figure S3e–l) had alleles that surfed on the eastern side of the geographic space, but not on the western side. Three of the surfing alleles were the top three contributors to sPCA axis 1 (alleles 209, 412 and 463).

Testing for selective neutrality among these microsatellite loci yielded different conclusions depending on the geographic span of individuals included in the tests. When groups of infrapopulations spanning long distances were included in an analysis, BAYESCAN indicated strong signatures of either population expansion or natural selection, factors that both yield F_{ST} outliers (Excoffier & Ray, 2008; Lotterhos & Whitlock, 2014). For example, when infrapopulations from T1–T3 and the five northernmost grid samples were included in an analysis, 10 of the 12 loci appeared as outliers at FDR = 0.05. Likewise, when all 26 grid infrapopulations were included in an analysis, 10 of the 12 loci examined appeared as outliers. Because range expansion is an inherent part of this study, we performed additional tests on three restricted locality groups: 2016 infrapopulations from La Joya (the core of the species distribution), T3 (a site that was

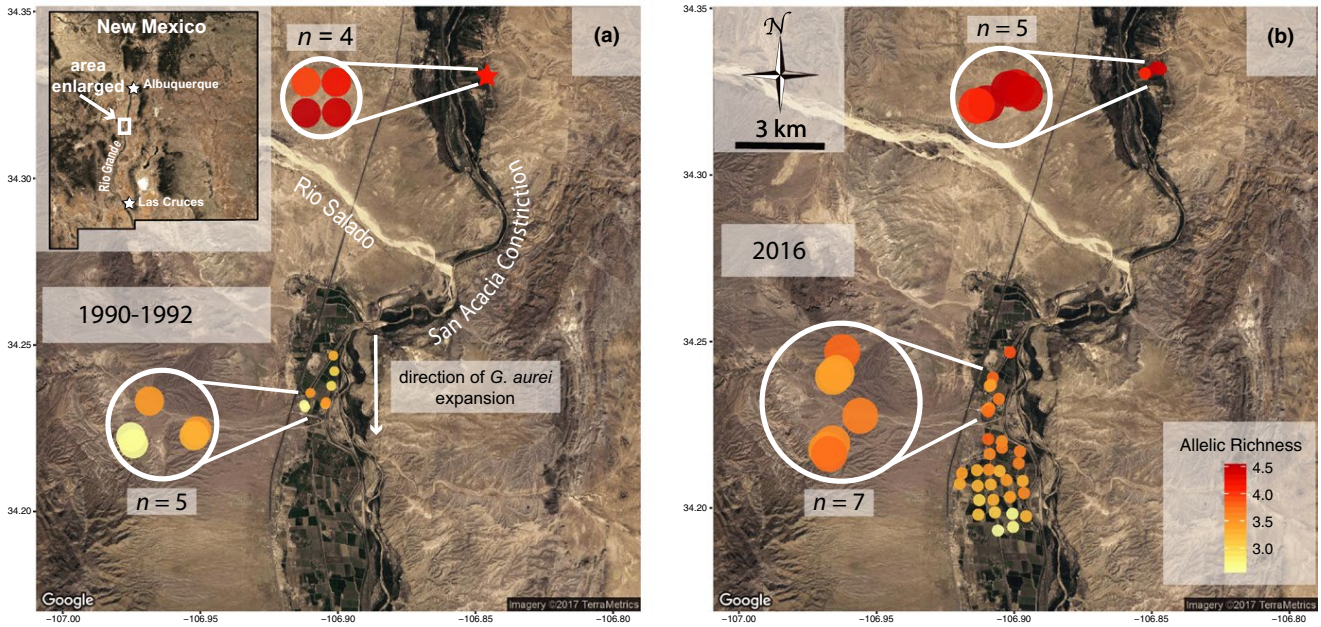


FIGURE 2 Infrapopulations of *Geomydoecus aurei* (mean *n* = 30 lice per coloured circle) sampled along the Rio Grande Valley of New Mexico in (a) 1990–1992 and (b) 2016. Outside the valley and where the green, irrigated valley is narrowed (the San Acacia constriction of the Rio Grande Valley), pocket gopher habitat is extremely limited and patchy, restricting host introgression (Smith et al., 1983) and opportunities for louse dispersal. However, *G. aurei* has expanded its range southward across this constriction likely in the last 100 years (Hafner et al., 1998). In 2016, the southern limit of the species distribution (southernmost circles of [b]) was approximately 3.5 km farther south than in 1990–1992 (southernmost circles of [a]), indicating an average southward movement of *G. aurei* of 150 m/year. Colour indicates allelic richness (AR) with dense red indicating maximum AR, which occurs in populations in the core of the *G. aurei* distribution. Colour becomes progressively more dilute as AR decreases in the newly invaded portions of the species range [Colour figure can be viewed at wileyonlinelibrary.com]

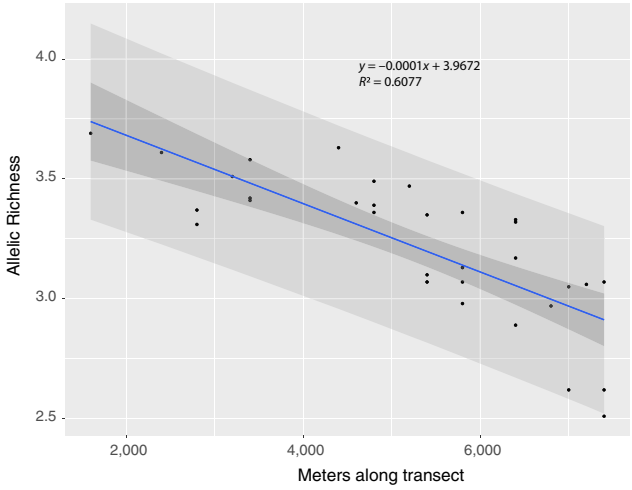


FIGURE 3 Regression analysis showing progressive loss of genetic diversity (allelic richness) in *Geomydoecus aurei* louse infrapopulations with increasing distance from the initial site of population establishment. Distance is given as meters along a collecting transect that runs from the initial site of population colonization (0 m) through the zone of population expansion, a maximum distance of 7,400 m to the south ($F = 49.6$, $p < 0.001$); 95% confidence intervals are given for the line and for the points (dark grey and light grey, respectively) [Colour figure can be viewed at wileyonlinelibrary.com]

colonized in approximately 1991) and four infrapopulations collected in 2016 at the forefront of the ongoing range expansion (grid cells 23–25 and 28). For these three restricted regions, no loci showed F_{ST} outliers, suggesting selective neutrality of the alleles. Therefore, when the effects of the documented population expansion in this system are controlled for, these tests suggest selective neutrality.

4 | DISCUSSION

4.1 | Effects of linear spatial expansion

The effects of genetic drift on populations at the periphery of a species range have long been recognized (Mayr, 1942). Austerlitz et al. (1997) highlighted the consequences of founder effects on an expanding population, showing that, as demes are established one after another in a one-dimensional stepping stone model, successive founder events will progressively decrease genetic diversity as a result of genetic drift that increases with distance of a new deme from the source population. Our genetic data from the ongoing range expansion of *G. aurei* clearly demonstrate this pattern of decreasing genetic diversity in a natural setting with parasites that colonize new hosts infrequently (Demastes et al., 1998) and are distributed over the very patchy islands of habitat provided to them by their hosts.

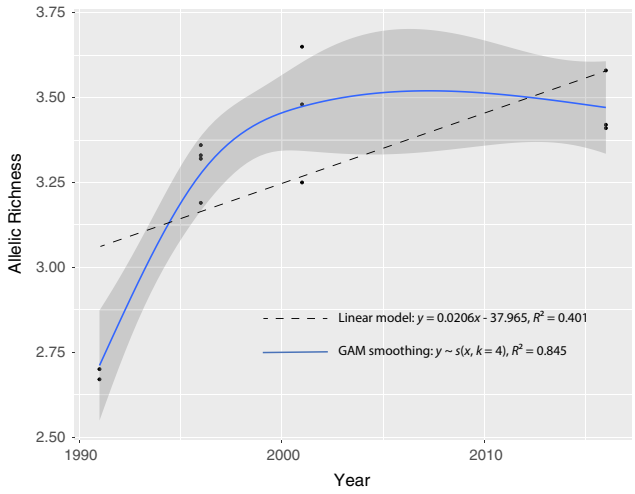


FIGURE 4 Infrapopulation allelic richness over time at a single collection site with regression line (and 95% confidence interval for the line) drawn using a generalized additive model to compensate for the non-linear relationship between time for recovery and allelic richness (F = 19.7, p < 0.001). Populations sampled in 1991 were collected soon after the initial establishment of *Geomydoecus aurei* at site T3 (Figure 1). Genetic recovery from the initial population bottleneck began quickly (in the first 5 years or 45 louse generations), but then tapered off. At last sampling, 25 years or 225 louse generations after population establishment, infrapopulations had failed to reach the level of genetic diversity observed in infrapopulations of lice from the core of the species distribution. A linear model (dotted line) also indicates a significant relationship between allelic richness and time for recovery [Colour figure can be viewed at wileyonlinelibrary.com]

Infrapopulations of lice from the area of population expansion south of the San Acacia constriction had lower genetic diversity than did infrapopulations from the core of the species distribution north of the constriction in several measures and over two different points in time (Figure 2). Therefore, as predicted, the process of population expansion has decreased genetic diversity substantially.

The process of population expansion has not, however, had any apparent effect on infrapopulation F_{IS}, which is near zero for every infrapopulation of lice tested here (Table 1). This finding is somewhat surprising given the tendency towards inbreeding of parasite populations (Nadler, 1995; Nessner et al., 2014), and it suggests that chewing louse infrapopulations are large enough at initial host colonization and mobile enough on a single host to avoid substantial inbreeding even in the face of population expansion into a new area.

Within the zone of population expansion, considering only lice from south of the San Acacia constriction, there also was a clear decrease in AR with increasing distance from the source population (Figures 2 and 3). This pattern of decreasing diversity is consistent with a one-dimensional stepping stone model of colonization with repeated population bottlenecks. Genetic diversity, as measured by expected heterozygosity, also showed this relationship despite the fact that ample theoretical and experimental evidence indicates that bottlenecks generally will have a more direct effect on the presence or absence of alleles than on heterozygosity (Greenbaum, Templeton, Zarmi, & Bar-David, 2014; Leberg, 1992, 2002; Nei et al., 1975; Spencer, Neigel, & Leberg, 2000; Swaegers et al., 2013), making AR a more sensitive measure of genetic diversity than H_E for these analyses. Thus, the decrease in genetic diversity that we observed with distance from the core population in this ongoing range expansion provides independent validation of approaches that infer recent population expansion from observed decreases in genetic diversity over geography (e.g., Jezkova et al., 2015; Schregel, Kopatz, Eiken, Swenson, & Hagen, 2017) and verification of approaches that infer alternative colonization dynamics

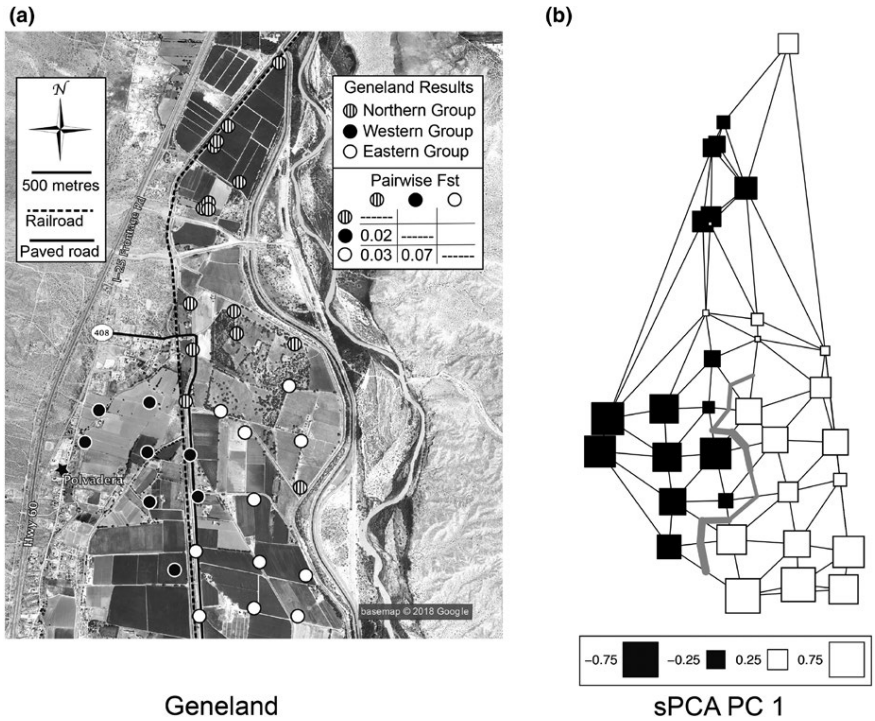


FIGURE 5 Spatial analyses of allele frequencies in infrapopulations of *Geomydoecus aurei* south of the San Acacia constriction, where the species has recently expanded its range. (a) Geneland and (b) spatial PCA (sPCA) results for principal component 1 (PC 1) mapped over geography. Size and colour of boxes indicate infrapopulation eigenvalues along PC 1. Lines between boxes show Delaunay triangulation connection grids used in Monmonier analysis and sPCA. Jagged grey lines indicate results of Monmonier barrier analysis with thickness of the line showing relative magnitude of genetic distance. The east–west partitioning of genetic diversity detected by each of these analyses in the southern grid infrapopulation samples is consistent with expectations for expanding populations

from the absence of such a pattern (e.g., Berthouly-Salazar et al., 2013; Becheler et al., 2016).

4.2 | Recovery of genetic diversity

Population connectivity can be a powerful force in rescuing AR after a population bottleneck, with some genetic recoveries in highly connected populations occurring in as little as one or two generations (Jangjoo, Matter, Roland, & Keyghobadi, 2016; McEachern, Vuren, Floyd, May, & Eadie, 2011). However, simulation studies have indicated that the effects of founder events can persist for hundreds, even thousands, of generations when founding populations reproduce and expand in numbers prior to exchanging migrants with other newly established populations (Boileau, Hebert, & Schwartz, 1992; Ibrahim et al., 1996). Over a 25-year time span (about 225 louse generations), we observed a statistically significant 32% increase in genetic diversity. However, we did not observe any infrapopulations in the zone of population expansion with genetic diversity values equivalent to those in the core of the species distribution, indicating that recovery is not yet complete 225 generations after population establishment.

Almost 80% of the genetic recovery observed at the T3 locality (Figure 4) happened within the first 5 years (45 louse generations) after establishment of the new *G. aurei* infrapopulations. This initially rapid increase in genetic diversity following infrapopulation bottlenecks almost certainly results from gene flow among the recently bottlenecked *G. aurei* infrapopulations. Because some alleles from the core population likely were lost during the bottleneck event that occurred during initial population establishment south of the San Acacia constriction, we believe these infrapopulations will be unable to return to pre-bottleneck AR without further incorporation of new alleles either by immigration or mutation. Thus, we expect that any further increase in genetic diversity in the T3 infrapopulations, potentially to the point of reaching core-population levels of AR, will be slow and gradual, barring an increase in rate of immigration from the core population or an increase in rate of accumulation of new alleles via mutation. Immigration of lice from north of the constriction would be the most likely source of new alleles, and the lack of full genetic recovery that we observe here probably indicates a lack of significant current gene flow from northern louse populations into the area of current population expansion.

It has been firmly established that, in expanding populations, the cascading effects of repeated bottlenecks in founding populations derived from recently bottlenecked parental populations can reduce genetic diversity rapidly due to drift (Excoffier et al., 2009). This diminution of genetic diversity by serial bottlenecking likely explains the pattern of decreased genetic diversity we observed in louse infrapopulations with increased distance from the source population. However, genetic recovery, even partial genetic recovery, also contributes to the observed pattern of decreased genetic diversity with increased distance from the source population because infrapopulations located closer to the source population had a longer time to recover genetically than those further from the source population. Thus, the normally opposing forces of drift and recovery have worked together to produce the overarching genetic pattern of reduced diversity with increased distance observed in this zone of expansion.

4.3 | Allele surfing

All analyses suggest a lack of population structure in the non-expanding pocket gopher population, indicating that the four-tier potential barrier to gene flow (Figure 5a) had no measurable influence on pocket gopher population structure. These animals likely have been established in this area since intensive agriculture began. This long establishment, coupled with the spatial scale of the analysis, which spans only 6 km for a host that has an average annual dispersal distance of approximately 400 m per year (Hafner et al., 1998), makes it unsurprising that these hosts show evidence of panmixia.

Louse population structure appears independent from host population structure. Mantel analyses indicate no significant relationship between host genetic distance and parasite genetic distance. However, the four-tier partial reflective boundary made up by the road, drainage ditches, and railroad may have acted to enhance differentiation in the expanding louse population as different alleles gained opportunities to surf (and as genetic drift also operated) on opposite sides of the barrier in these newly expanding louse populations. In the expanding population of chewing lice, we observed a pattern of east–west genetic differentiation that was detectable with Geneland, sPCA and Monmonier barrier detection. Lice collected in the central-most column of grid cells all came either from the east side of the four-tier reflective boundary or from within it (i.e., west of the paved road, but east of the railroad), but the eastern and western genetic groups of lice observed here are only partially coincident with the four-tier barrier to gene flow. Therefore, the four-tier partial reflective boundary appears permeable to gene flow among lice, facilitated by the occasional dispersing pocket gopher (Figure 5a).

The process of population expansion has been demonstrated to generate genetic patterns within populations with genetic differentiation arising in sectors parallel with the axis of population expansion, detectable in axis 1 of principal components analysis (François et al., 2010). This pattern is expected to be compounded when a partial geographic barrier to gene flow allows different alleles to surf on opposite sides of the barrier, with the degree of genetic differentiation increasing the longer surfing along the barrier continues (Novembre & Di Rienzo, 2009; Peischl et al., 2016, pp. 54–55, Figures 1c and 2). Our tests of genetic variation over geography in a population that is experiencing an ongoing, documented spatial expansion provide empirical evidence of the powerful effect that surfing can have on genetic structure in expanding populations. Of 12 loci examined, six showed an allele that surfed to high frequency on one or both sides of the zone of expansion. These surfing alleles were top contributors to the genetic structure determined by sPCA for these lice, providing a mechanism and empirical support for past studies that have shown genetic structure as a signature of surfing in expanding populations (François et al., 2010; Pereira et al., 2018). Interestingly, the genetic

patterns generated in these expanding populations (Figure 5) reflected quite closely the patterns envisioned for idealized populations by Peischl et al. (2016, pp. 54–55, Figures 1c and 2) with greater population subdivision being observed between lice sampled nearer the wave front, where surfing has occurred over the longest geographic distance and for the greatest number of generations (Figure 5b).

Allele surfing has potential negative fitness consequences for expanding populations (Bosshard et al., 2017; Klopfstein et al., 2006; Peischl, Dupanloup, Kirkpatrick, & Excoffier, 2013; Peischl & Excoffier, 2015; Willi, Fracassetti, Zoller, & Buskirk, 2018). Alternatively, beneficial mutations may surf to fixation in the zone of population expansion (Gralka et al., 2016; Lehe, Hallatschek, & Peliti, 2012). Alleles at the 12 microsatellite loci we examined here appeared selectively neutral, so this study documents surfing of neutral alleles in a natural population. However, when studied over larger transects, these same loci show strong patterns of F_{ST} outliers; this pattern is expected for expanding populations, but this study provides a reminder that F_{ST} outlier tests will provide results that can be mistaken for adaptive change in expanding populations (Excoffier & Ray, 2008; Lotterhos & Whitlock, 2014).

5 | CONCLUSIONS

This study provides novel empirical confirmation of theoretical models that predict the effects of population expansion on genetics studied in hundreds of individuals over hundreds of generations. Rather than examining the genetic impact of expansion in populations long after the expansion process has been completed, here we have examined transects through natural populations at times up to 25 years (225 generations) apart during an ongoing population expansion. We showed that successive founder events have progressively reduced genetic diversity as populations have been established farther from the population core. We also documented partial recovery of lost genetic diversity by studying populations of individuals sampled in the same geographic area at four time points: first at initial population establishment (1991), then about 5 years later, 10 years later and 25 years later. Mean AR of the infrapopulations increased rapidly after initial population establishment, but then recovery stalled with diversity values never reaching the level of genetic diversity observed in the core of the species distribution, consistent with models that suggest that the effects of drift can persist for hundreds or thousands of generations in certain conditions (Boileau et al., 1992; Ibrahim et al., 1996). Finally, we document a clear signal of genetic structure in this expanding population that is not derived from selection or from a long history of isolation, but that is instead derived from genetic drift and the surfing of alleles during the expansion process.

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AUTHOR CONTRIBUTIONS

T.A.S. and J.W.D. conceived of the study design in consultation with D.J.H., M.S.H. and J.E.L. Funding was secured by J.W.D., J.E.L. and T.A.S. All authors participated in specimen collection, with D.J.H. planning field efforts to locate the current southern edge of population expansion and to plot the 2016 sampling grid. J.W.D. identified louse species and led DNA extraction and louse vouchering. T.A.S. was responsible for microsatellite data collection and processing. Louse statistical analyses were performed by J.W.D., and pocket gopher data analysis was performed by T.A.S. All authors participated in writing the manuscript.

DATA ACCESSIBILITY

Chewing louse microsatellite genotypes, allele frequencies and R-scripts are available in Dryad, https://doi.org/10.5061/dryad.63p479j. Parasite voucher specimens are preserved at the University of Northern Iowa. Pocket gopher voucher specimens are housed at the Louisiana State University Museum of Natural Science [LSUMZ], the Museum of Southwestern Biology [MSB] at the University of New Mexico, or the Biodiversity Research and Teaching Collections at Texas A&M University [BRTC]. Pocket gopher sequences are accessioned in GenBank (accessions MH558954–MH558992, MH559032–MH559070, MH559071–MH559109 and MH558993–MH559031). Sequence alignments, structure input files and GenePop files are available in Dryad, https://doi.org/10.5061/dryad.63p479j.

REFERENCES

Anscombe, F. J. (1953). Sequential estimation. *Journal of the Royal Statistical Society. Series B (Methodological)*, *15*, 1–29. https://doi.org/10.1111/j.2517-6161.1953.tb00121.x

Austerlitz, F., Jung-Muller, B., Godelle, B., & Gouyon, P. H. (1997). Evolution of coalescence times, genetic diversity and structure during colonization. *Theoretical Population Biology*, *51*, 148–164. https://doi.org/10.1006/tpbi.1997.1302

Becheler, R., Xhaard, C., Klein, E. K., Hayden, K. J., Frey, P., De Mita, S., & Halkett, F. (2016). Genetic signatures of a range expansion in natura: When clones play leapfrog. *Ecology and Evolution*, *6*, 6625–6632. https://doi.org/10.1002/ece3.2392

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, *57*, 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Berthouly-Salazar, C., Hui, C., Blackburn, T. M., Gaboriaud, C., Rensburg, B. J., Vuuren, B. J., & Roux, J. J. (2013). Long-distance dispersal maximizes evolutionary potential during rapid geographic range expansion. *Molecular Ecology*, *22*, 5793–5804. https://doi.org/10.1111/mec.12538

Bock, D. G., Caseys, C., Cousens, R. D., Hahn, M. A., Heredia, S. M., Hübner, S., … Rieseberg, L. H. (2015). What we still don't know about invasion genetics. *Molecular Ecology*, *24*, 2277–2297. https://doi.org/10.1111/mec.13032

Boileau, M. G., Hebert, P. D., & Schwartz, S. S. (1992). Non-equilibrium gene frequency divergence: Persistent founder effects in natural populations. *Journal of Evolutionary Biology*, *5*, 25–39. https://doi.org/10.1046/j.1420-9101.1992.5010025.x

Bosshard, L., Dupanloup, I., Tenaillon, O., Bruggmann, R., Ackermann, M., Peischl, S., & Excoffier, L. (2017). Accumulation of deleterious mutations during bacterial range expansions. *Genetics*, *207*, 669–684. https://doi.org/10.1534/genetics.117.300144

Burton, O. J., & Travis, J. M. J. (2008). Landscape structure and boundary effects determine the fate of mutations occurring during range expansions. *Heredity*, *101*, 329–340.

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*, 1024–1026. https://doi.org/10.1126/science.1206432

Corander, J., Marttinen, P., Sirén, J., & Tang, J. (2008). Enhanced Bayesian modelling in BAPS software for learning genetic structures of populations. *BMC Bioinformatics*, *9*, 539.

Cwynar, L. C., & MacDonald, G. M. (1987). Geographical variation of lodgepole pine in relation to population history. *The American Naturalist*, *129*, 463–469. https://doi.org/10.1086/284651

Demastes, J. W. (1990). Host-parasite coevolutionary relationships in two assemblages of pocket gophers and chewing lice. MS thesis, Louisiana State University, Baton Rouge, LA.

Demastes, J. W. (1996). Analysis of host-parasite cospeciation: effects of spatial and temporal scale. PhD dissertation, Louisiana State University, Baton Rouge, LA.

Demastes, J. W., Hafner, M. S., Hafner, D. J., & Spradling, T. A. (1998). Pocket gophers and chewing lice: A test of the maternal transmission hypothesis. *Molecular Ecology*, *7*, 1065–1069. https://doi.org/10.1046/j.1365-294x.1998.00383.x

Dray, S., & Dufour, A. B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*, 1–20.

Eckert, K. A., & Hile, S. E. (2009). Every microsatellite is different: Intrinsic DNA features dictate mutagenesis of common microsatellites present in the human genome. *Molecular Carcinogenesis*, *48*, 379–388.

Edmonds, C. A., Lillie, A. S., & Cavalli-Sforza, L. L. (2004). Mutations arising in the wave front of an expanding population. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 975–979. https://doi.org/10.1073/pnas.0308064100

Edwards, A. W. F. (1971). Distance between populations on the basis of gene frequencies. *Biometrics*, *27*, 873–881.

Ellegren, H. (2004). Microsatellites: Simple sequences with complex evolution. *Nature Reviews*, *5*, 435–443. https://doi.org/10.1038/nrg1348

Esch, G. W., Gibbons, J. W., & Bourque, J. E. (1975). An analysis of the relationship between stress and parasitism. *American Midland Naturalist*, *93*, 339–353. https://doi.org/10.2307/2424167

Excoffier, L., Foll, M., & Petit, R. (2009). Genetic consequences of range expansion. *Annual Review of Ecology and Systematics*, *40*, 481–501.

Excoffier, L., & Ray, N. (2008). Surfing during population expansions promotes genetic revolutions and structuration. *Trends in Ecology and Evolution*, *23*, 347–351. https://doi.org/10.1016/j.tree.2008.04.004

Falush, D., Stephens, M., & Pritchard, J. K. (2003). Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. *Genetics*, *164*, 1567–1587.

Faria, N. R., Rambaut, A., Suchard, M. A., Baele, G., Bedford, T., Ward, M. J., … Posada, D. (2014). The early spread and epidemic ignition of HIV-1 in human populations. *Science*, *346*, 56–61. https://doi.org/10.1126/science.1256739

Foll, M., & Gaggiotti, O. E. (2008). A genome scan method to identify selected loci appropriate for both dominant and codominant markers: A Bayesian perspective. *Genetics*, *180*, 977–993. https://doi.org/10.1534/genetics.108.092221

François, O., Currat, M., Ray, N., Han, E., Excoffier, L., & Novembre, J. (2010). Principal component analysis under population genetic models of range expansion and admixture. *Molecular Biology and Evolution*, *27*, 1257–1268. https://doi.org/10.1093/molbev/msq010

Fusco, D., Gralka, M., Kayser, J., Anderson, A., & Hallatschek, O. (2016). Excess of mutational jackpot events in expanding populations revealed by spatial Luria-Delbruck experiments. *Nature Communications*, *7*, 12760.

Glaubitz, J. (2004). CONVERT: A user-friendly program to reformat diploid genotypic data for commonly used population genetic software packages. *Molecular Ecology Notes*, *4*, 309–310. https://doi.org/10.1111/j.1471-8286.2004.00597.x

Graciá, E., Botella, F., Anadón, J. D., Edelaar, P., Harris, D. J., & Giménez, A. (2013). Surfing in tortoises? Empirical signs of genetic structuring owing to range expansion. *Biology Letters*, *9*, 20121091. https://doi.org/10.1098/rsbl.2012.1091

Gralka, M., Stiewe, F., Farrell, F., Moebius, W., Waclaw, B., & Hallatschek, O. (2016). Allele surfing promotes microbial adaptation from standing variation. *Ecology Letters*, *19*, 889–898. https://doi.org/10.1111/ele.12625

Greenbaum, G., Templeton, A. R., Zarmi, Y., & Bar-David, S. (2014). Allelic richness following population founding events – A stochastic modeling framework incorporating gene flow and genetic drift. *PLoS ONE*, *9*, e115203. https://doi.org/10.1371/journal.pone.0115203

Guillot, G., Mortier, F., & Estoup, A. (2005). GENELAND: A computer package for landscape genetics. *Molecular Ecology Notes*, *5*, 712–715.

Hafner, D. J., Hafner, M. S., Spradling, T. A., Light, J. E., & Demastes, J. W. (2018) Temporal and spatial dynamics of competitive parapatry in chewing lice. Manuscript submitted for publication.

Hafner, M. S., Demastes, J. W., Hafner, D. J., Spradling, T. A., Sudman, P. D., & Nadler, S. A. (1998). Age and movement of a hybrid zone: Implications for dispersal distance in pocket gophers and their chewing lice. *Evolution*, *52*, 278–282. https://doi.org/10.1111/j.1558-5646.1998.tb05164.x

Hafner, M. S., Demastes, J. W., Spradling, T. A., & Reed, D. L. (2003). Cophylogeny between pocket gophers and chewing lice. In R. D. M.Page (Ed.), *Tangled trees: Phylogeny, cospeciation, and coevolution* (pp. 195–218). Chicago, IL: University of Chicago Press.

Hale, M. L., Burg, T. M., & Steeves, T. E. (2012). Sampling for microsatellite-based population genetic studies: 25 to 30 individuals per population is enough to accurately estimate allele frequencies. *PLoS ONE*, *7*, e45170. https://doi.org/10.1371/journal.pone.0045170

Hallatschek, O., Hersen, P., Ramanathan, S., & Nelson, D. R. (2007). Genetic drift at expanding frontiers promotes gene segregation. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 19926–19930. https://doi.org/10.1073/pnas.0710150104

Harper, S. E., Spradling, T. A., Demastes, J. W., & Calhoun, C. S. (2015). Host behaviour drives parasite genetics at multiple geographic scales: Population genetics of the chewing louse, *Thomomydoecus minor*. *Molecular Ecology*, *24*, 4129–4144.

Hewitt, G. M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, *58*, 247–276. https://doi.org/10.1111/j.1095-8312.1996.tb01434.x

Hubisz, M. J., Falush, D., Falush, D., Stephens, M., & Prichard, J. K. (2009). Inferring weak population structure with the assistance of sample group information. *Molecular Ecology Resources*, *9*, 1322–1332. https://doi.org/10.1111/j.1755-0998.2009.02591.x

Ibrahim, K. M., Nichols, R. A., & Hewitt, G. M. (1996). Spatial patterns of genetic variation generated by different forms of dispersal. *Heredity*, *77*, 282–291.

Jangjoo, M., Matter, S. F., Roland, J., & Keyghobadi, N. (2016). Connectivity rescues genetic diversity after a demographic bottleneck in a butterfly population network. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 10914–10919. https://doi.org/10.1073/pnas.1600865113

Jezkova, T., Riddle, B. R., Card, D. C., Schield, D. R., Eckstut, M. E., & Castoe, T. A. (2015). Genetic consequences of postglacial range expansion in two codistributed rodents (genus *Dipodomys*) depend on ecology and genetic locus. *Molecular Ecology*, *24*, 83–97.

Jombart, T. (2008). adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics*, *24*, 1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Jombart, T., & Ahmed, I. (2011). adegenet 1.3-1: New tools for the analysis of genome-wide SNP data. *Bioinformatics*, *27*, 3070–3071. https://doi.org/10.1093/bioinformatics/btr521

Jombart, T., Devillard, S., Dufour, A. B., & Pontier, D. (2008). Revealing cryptic spatial patterns in genetic variability by a new multivariate method. *Heredity*, *101*, 92–103. https://doi.org/10.1038/hdy.2008.34

Jombart, T., Pontier, D., & Dufour, A. B. (2009). Genetic markers in the playground of multivariate analysis. *Heredity*, *102*, 330–341. https://doi.org/10.1038/hdy.2008.130

Jones, K., & Almond, S. (1992). Moving out of the linear rut: The possibilities of generalized additive models. *Transactions of the Institute of British Geographers*, *17*, 434–447. https://doi.org/10.2307/622709

Kahle, D., & Wickham, H. (2013). ggmap: Spatial visualization with ggplot2. *The R Journal*, *5*, 144–161.

Kalinowski, S. T. (2004). Counting alleles with rarefaction: Private alleles and hierarchical sampling designs. *Conservation Genetics*, *5*, 539–543. https://doi.org/10.1023/B:COGE.0000041021.91777.1a

Keenan, K., McGinnity, P., Cross, T. F., Crozier, W. W., & Prodöhl, P. A. (2013). diveRsity: An R package for the estimation of population genetics parameters and their associated errors. *Methods in Ecology and Evolution*, *4*, 782–788.

Klopfstein, S., Currat, M., & Excoffier, L. (2006). The fate of mutations surviving on the wave of a range expansion. *Molecular Biology and Evolution*, *23*, 482–490.

Leberg, P. L. (1992). Effects of population bottlenecks on genetic diversity as measured by allozyme electrophoresis. *Evolution*, *46*, 477–494. https://doi.org/10.1111/j.1558-5646.1992.tb02053.x

Leberg, P. L. (2002). Estimating allelic richness: Effects of sample size and bottlenecks. *Molecular Ecology*, *11*, 2445–2449. https://doi.org/10.1046/j.1365-294X.2002.01612.x

Lehe, R., Hallatschek, O., & Peliti, L. (2012). The rate of beneficial mutations surfing on the wave of a range expansion. *PLoS Computational Biology*, *8*, e1002447. https://doi.org/10.1371/journal.pcbi.1002447

Light, J. E., Harper, S., Johnson, K., Demastes, J., & Spradling, T. (2018). Development and characterization of 12 novel polymorphic microsatellite loci for the mammal chewing louse *Geomydoecus aurei* (Insecta: Phthiraptera) and a comparison of next-generation sequencing approaches for use in parasitology. *Journal of Parasitology*, *104*, 89–95.

Lotterhos, K. E., & Whitlock, M. C. (2014). Evaluation of demographic history and neutral parameterization on the performance of FST outlier tests. *Molecular Ecology*, *23*, 2178–2192.

Manni, F., Guerard, E., & Heyer, E. (2004). Geographic patterns of (genetic, morphologic, linguistic) variation: How barriers can be detected by using Monmonier's algorithm. *Human Biology*, *76*, 173–190. https://doi.org/10.1353/hub.2004.0034

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, *27*, 209–220.

Mayr, E. (1942). *Systematics and the origin of species*. New York, NY: Columbia University Press.

McEachern, M. B., Van Vuren, D. H., Floyd, C. H., May, B., & Eadie, J. M. (2011). Bottlenecks and rescue effects in a fluctuating population of golden-mantled ground squirrels (*Spermophilus lateralis*). *Conservation Genetics*, *12*, 285–296. https://doi.org/10.1007/s10592-010-0139-z

Meirmans, P. G. (2012). The trouble with isolation by distance. *Molecular Ecology*, *21*, 2839–2846. https://doi.org/10.1111/j.1365-294X.2012.05578.x

Monmonier, M. S. (1973). Maximum-difference barriers: An alternative numerical regionalization method. *Geographical Analysis*, *5*, 245–261. https://doi.org/10.1111/j.1538-4632.1973.tb01011.x

Nadler, S. A. (1995). Microevolution and the genetic structure of parasite populations. *The Journal of Parasitology*, *81*, 395–403. https://doi.org/10.2307/3283821

Nadler, S. A., Hafner, M. S., Hafner, J. C., & Hafner, D. J. (1990). Genetic differentiation among chewing louse populations (Mallophaga: Trichodectidae) in a pocket gopher contact zone (Rodentia: Geomyidae). *Evolution*, *44*, 942–951. https://doi.org/10.1111/j.1558-5646.1990.tb03816.x

Nei, M., Maruyama, T., & Chakraborty, R. (1975). The bottleneck effect and genetic variability in populations. *Evolution*, *29*, 1–10. https://doi.org/10.1111/j.1558-5646.1975.tb00807.x

Nessner, C. E., Andersen, J. J., Renshaw, M. A., Giresi, M. M., & Light, J. E. (2014). Characterization of 17 novel polymorphic microsatellite loci in the mammal chewing louse *Geomydoecus ewingi* (Insecta: Phthiraptera) for population genetic analyses. *The Journal of Parasitology*, *100*, 873–877.

Novembre, J., & Di Rienzo, A. (2009). Spatial patterns of variation due to natural selection in humans. *Nature Reviews Genetics*, *10*, 745. https://doi.org/10.1038/nrg2632

Pauls, S. U., Nowak, C., Bálint, M., & Pfenninger, M. (2013). The impact of global climate change on genetic diversity within populations and species. *Molecular Ecology*, *22*, 925–946. https://doi.org/10.1111/mec.12152

Peischl, S., Dupanloup, I., Bosshard, L., & Excoffier, L. (2016). Genetic surfing in human populations: From genes to genomes. *Current Opinion in Genetics & Development*, *41*, 53–61. https://doi.org/10.1016/j.gde.2016.08.003

Peischl, S., Dupanloup, I., Kirkpatrick, M., & Excoffier, L. (2013). On the accumulation of deleterious mutations during range expansions. *Molecular Ecology*, *22*, 5972–5982. https://doi.org/10.1111/mec.12524

Peischl, S., & Excoffier, L. (2015). Expansion load: Recessive mutations and the role of standing genetic variation. *Molecular Ecology*, *24*, 2084–2094. https://doi.org/10.1111/mec.13154

Peischl, S., Dupanloup, I., Foucal, A., Jomphe, M., Braut, V., Grenier, J.-C., … Excoffier, L. (2018). Relaxed selection during a recent human expansion. *Genetics*, *208*, 763–777. https://doi.org/10.1534/genetics.117.300551

Pereira, P., Teixeira, J., & Velo-Antón,, (2018). Allele surfing shaped the genetic structure of the European pond turtle via colonization and population expansion across the Iberian Peninsula from Africa. *Journal of Biogeography*, *45*, 2202–2215. https://doi.org/10.1111/jbi.13412

Pierce, A. A., Zalucki, M. P., Bangura, M., Udawatta, M., Kronforst, M. R., Altizer, S., … de Roode, J. C. (2014). Serial founder effects and genetic differentiation during worldwide range expansion of monarch butterflies. *Proceedings of the Royal Society of London B: Biological Sciences*, *281*, 20142230. https://doi.org/10.1098/rspb.2014.2230

Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. *R News*, *6*, 7–11.

Price, R. D., & Hellenthal, R. A. (1981). A review of the *Geomydoecus californicus* complex (Mallophaga: Trichodectidae) from *Thomomys* (Rodentia: Geomyidae). *Journal of Medical Entomology*, *18*, 1–23.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*, 945–959.

R Core Team (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/.

Reed, D. L., & Hafner, M. S. (1997). Host specificity of chewing lice on pocket gophers: A potential mechanism for cospeciation. *Journal of Mammalogy*, *78*, 655–660. https://doi.org/10.2307/1382916

Roques, L., Garnier, J., Hamel, F., & Klein, E. K. (2012). Allee effect promotes diversity in traveling waves of colonization. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 8828–8833. https://doi.org/10.1073/pnas.1201695109

RStudio Team. (2016). *RStudio: Integrated development for R*. Boston, MA: RStudio Inc. https://www.rstudio.com/products/rstudio/.

Rust, R. W. (1974). The population dynamics and host utilization of *Geomydoecus oregonus*, a parasite of *Thomomys bottae*. *Oecologia*, *15*, 287–304. https://doi.org/10.1007/BF00345184

Safner, T., Miller, M. P., McRae, B. H., Fortin, M. J., & Manel, S. (2011). Comparison of Bayesian clustering and edge detection methods for inferring boundaries in landscape genetics. *International Journal of Molecular Sciences*, *12*, 865–889. https://doi.org/10.3390/ijms12020865

Schregel, J., Kopatz, A., Eiken, H. G., Swenson, J. E., & Hagen, S. B. (2017). Sex-specific genetic analysis indicates low correlation between demographic and genetic connectivity in the Scandinavian brown bear (*Ursus arctos*). *PLoS ONE*, *12*, e0180701. https://doi.org/10.1371/journal.pone.0180701

Sikes, R. S. & The Animal Care and Use Committee of the American Society of Mammalogists (2016). 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, *97*, 663–688. https://doi.org/10.1093/jmammal/gyw078

Slatkin, M., & Excoffier, L. (2012). Serial founder effects during range expansion: A spatial analog of genetic drift. *Genetics*, *191*, 171–181. https://doi.org/10.1534/genetics.112.139022

Smith, M. F., Patton, J. L., Hafner, J. C., & Hafner, D. J. (1983). *Thomomys bottae* pocket gophers in the central Rio Grande Valley, New Mexico: Local differentiation, gene flow, and historical biogeography. *Occasional Papers of the Museum of Southwestern Biology, University of New Mexico, Albuquerque*, *2*, 1–16.

Spencer, C. C., Neigel, J. E., & Leberg, P. L. (2000). Experimental evaluation of the usefulness of microsatellite DNA for detecting demographic bottlenecks. *Molecular Ecology*, *910*, 1517–1528. https://doi.org/10.1046/j.1365-294x.2000.01031.x

Streicher, J. W., McEntee, J. P., Drzich, L. C., Card, D. C., Schield, D. R., Smart, U., … Castoe, T. A. (2016). Genetic surfing, not allopatric divergence, explains spatial sorting of mitochondrial haplotypes in venomous coralsnakes. *Evolution*, *70*, 1435–1449. https://doi.org/10.1111/evo.12967

Swaegers, J., Mergeay, J., Therry, L., Larmuseau, M. H. D., Bonte, D., & Stoks, R. (2013). Rapid range expansion increases genetic differentiation while causing limited reduction in genetic diversity in a damselfly. *Heredity*, *111*, 422–429. https://doi.org/10.1038/hdy.2013.64

Taylor, L. H., Latham, S. M., & Mark, E. J. (2001). Risk factors for human disease emergence. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *356*, 983–989. https://doi.org/10.1098/rstb.2001.0888

Waters, J. M., Fraser, C. I., & Hewitt, G. M. (2013). Founder takes all: Density-dependent processes structure biodiversity. *Trends in Ecology & Evolution*, *28*, 78–85. https://doi.org/10.1016/j.tree.2012.08.024

Wheeler, R. E. (2010). multResp() lmPerm. The R project for statistical computing. http://www.r-project.org/.

White, T. A., Perkins, S. E., Heckel, G., & Searle, J. B. (2013). Adaptive evolution during an ongoing range expansion: The invasive bank vole (*Myodes glareolus*) in Ireland Molecular. *Ecology*, *22*, 2971–2985.

Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. New York, NY: Springer-Verlag.

Willi, Y., Fracassetti, M., Zoller, S., & Van Buskirk, J. (2018). Accumulation of mutational load at the edges of a species range. *Molecular Biology and Evolution*, *3*, 781–791. https://doi.org/10.1093/molbev/msy003

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society. Series B (Methodological)*, *73*, 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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