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ORIGINAL ARTICLE

Assessing the complex relationship between landscape, gene flow, and range expansion of a Mediterranean carnivore

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Abstract

Landscape resistance is often disregarded in studies of range expansions and population connectivity. To assess those effects, we simulated the expansion of the Egyptian mongoose (*Herpestes ichneumon*) in relation to landscape resistance through kernel resistance modeling, confronting it with previously published data regarding the observed pattern of expansion and genetic diversity of the population in Portugal. We modeled population expansion as a function of shrub cover and elevation through iterative simulation of a resistance model and a null model. We then performed an overlap analysis to assess the congruence between the observed pattern of expansion and both resistance and null models across 30 years. We also tested whether there is an effect of allelic surfing or the central-marginal hypothesis by correlating observed allelic richness (1) with the number of simulated years that each location with sampled genotypes had been occupied by the mongoose population and (2) with the cumulative resistant kernel density (which is a measure of population centrality). Results indicated a higher similarity between observed range expansion and the simulation using the null model and a marginally significant correlation between observed allelic richness and number of years of the simulated presence of the species in the null model. The pattern of range expansion in this population is most consistent with a neutral model of uniform resistance, and genetic diversity is most correlated with null model as well. This suggests that range expansion and genetic diversity patterns in expanding populations may not always be predicted by landscape resistance models developed through association of observed genetic differentiation with landscape features.

Keywords Egyptian mongoose · Genetic diversity · Landscape resistance · Range shifts · UNICOR

Introduction

The dynamics of landscape connectivity results from the complex and often unpredictable interaction between biotic and environmental factors (Clobert 2012; Wasserman et al. 2012; Baguette et al. 2013; Cushman et al. 2013; Cushman et al. 2014). Landscape resistance directly affects population connectivity, the latter being critical not only for maintaining the viability of spatially structured populations, but also for species to shift their geographic range in response to global change (Heller and Zavaleta 2009; Cushman et al. 2014). The inseparable relation between population connectivity and landscape resistance suggests that researchers should apply methods that explicitly predict changes in species distribution as functions of the interaction of population demographics and landscape patterns.

Landscape genetics methods enable analysis of the relationships between landscape patterns and the genetic differentiation and gene flow of species (Manel et al. 2003; Balkenhol et al. 2015), providing the capability to evaluate a large spectrum of hypotheses (Cushman et al. 2006, Cushman et al. 2013; Shirk et al. 2010; Castillo et al. 2014). Simultaneously, resistant kernel modeling has emerged as a particularly powerful approach to estimate the effects of different landscape features on movement

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and connectivity within and between populations (Compton et al. 2007; Cushman and Lewis 2010; Cushman and Landguth 2010, 2012; Cushman et al. 2016).

Investigating the relationship between population connectivity and landscape structure is even more critical for studying species experiencing range expansion, as they offer the opportunity to assess real-time impacts of landscape patterns on spatial processes of their population dynamics (Scheidt and Hurlbert 2014). Population expansion is greatly influenced by environmental factors (Lubina and Levin 1988); yet, other forces inherent to the population itself also drive patterns of species range expansion, e.g., ecological characteristics of the species, founder events, the dynamic pattern of contagious population spread from the initial site of colonization, the interaction with heterospecific competitors, and the long-distance founder events that originate new subpopulations (Cushman 2015).

Recently, the resistant kernel methodology was applied to range expansion by Cushman (2015). The author used UNICOR software (Landguth et al. 2012) to model the expansion of the invasive Asian tiger mosquito (*Aedes albopictus*). Resistant kernel modeling predicts the dispersal events frequency as a function of the source population size, location, and cumulative cost of movement through a given landscape (Cushman 2015). It provides smooth probability density predictions for movement patterns across complex landscapes (Landguth et al. 2012). The dynamic visualization of the results showed a contagious spread from an initial colonization site as a function of cumulative movement cost on a resistance surface and population growth around the initial colonization site. Also, the simulation showed a complex pattern of colonization of new areas through long-distance transport, followed by range expansion, vicariance, and secondary contact.

Landscape resistance is often disregarded when a range expansion event is documented and analyzed. However, without considering the spatially explicit landscape context of population spread, it is not possible to understand or predict patterns of range expansion (Cushman et al. 2013; Cushman et al. 2014). Moreover, in expanding populations, genetic variation may exhibit complex gradients across the species range, in which large effective population sizes (Ne) and gene flow lead to high genetic diversities in the core of the population, while marginal areas show lower values of genetic diversity (central-marginal hypothesis; Eckert et al. 2008). However, other patterns may appear due to the opposing dynamics at different range margins, leading to departures from the central-marginal hypothesis, specifically in expanding populations. The leading edge-rear model (Hampe and Petit 2005; Hewitt 2000) suggests that range expansion in the leading edges of a population may result in low genetic diversity due to the increasing of a certain number of individuals that undergo through long-distance dispersal events (allelic surfing; Hewitt 2000), while rear stable edges often reflect rich genetic diversity (Hampe and Petit 2005).

In this paper, we apply the resistant kernel approach to simulate the range expansion of the Egyptian mongoose (*Herpestes ichneumon*) in Portugal and describe the relationships between the expansion and the genetic patterns of the species under the influence of landscape structure. The Egyptian mongoose is often considered to be an exotic species in the Iberian Peninsula introduced by the Moors in the Middle Ages (Dobson 1998; Detry et al. 2011). Yet, a recent study showed that the Egyptian mongoose naturally settled in Iberia during the Late Pleistocene sea-level fluctuations (Gaubert et al. 2011). Since the 1980s, the species greatly expanded its territory from an initial population in southern Portugal (Barros 2009; Talegón and Parody 2009; Barros and Fonseca 2011; Balmori and Carbonell 2012). The expansion of the species was greatest between 1990 and 2000 and was driven by land-use changes related to increasing extent of shrub-dominated habitats and increasing temperatures, which consequently led to an increase of environmental favorability for the species (Barros 2009; Barros et al. 2015).

Most studies of range expansion focus on understanding rapid range expansions of invasive species during their process of invasion (With 2002; Urban et al. 2007; Kadoya and Washitani 2010). However, it is equally important to comprehend why a naturalized species that was confined for a long period within a specific range suddenly expands into new areas (e.g., Swenson et al. 1998; Putman and Moore 2010). This issue allied with unraveling the influence of landscape resistance during the expansion process can aid understanding of the mechanisms driving the expansion and a means to predict rates and patterns of future range shifts.

Analyzing the range expansion of the Egyptian mongoose offers a great opportunity to evaluate how well spatially explicit modeling of population spread as a function of landscape resistance predicts the actual pattern of an observed successful range expansion. The expansion of the species in Portugal is well documented, with records of the species distribution since 1980 to 2010. Also, it is known that the expansion was influenced by environmental variables (Barros et al. 2015) and gene flow is strongly influenced by the extent of shrub areas and altitude in Portugal (Barros et al. 2016a; see Appendix A for information regarding the genetic diversity of the species). Nonetheless, how landscape resistance shaped the expansion of the species on a yearly basis is unknown. Furthermore, understanding the relation between range expansion, landscape structure, and gene flow is a major challenge, especially in expanding populations where the dynamics between allelic patterns, heterozygosity, and dispersal are strongly and rapidly mutable (Cushman 2015), and local factors including migration events and the dynamics of the wave front can drastically influence the genetic patterns of expanding populations. In fact, spatial expansions can generate allele frequency gradients, promote allele surfing by introducing rare variants into newly occupied territories, creating distinct

and limited areas of low genetic diversity, or yielding to a massive introgression of local genes (Excoffier et al. 2009). Recent studies have shown that alleles with low frequency can surf on the wave of advance of an expansion event, reaching high frequencies and large areas (Excoffier and Ray 2008). Consistent with the central-marginal hypothesis, Bothwell et al. (2017) found that cottonwood trees had higher allelic richness in areas with high cumulative resistant kernel density, corresponding to locations with high population centrality and large amounts of gene flow.

Our main goal is to simulate population expansion of the Egyptian mongoose from an initial source area across a 30-year period and confront it with previously published information regarding the distribution, expansion, and genetic diversity of the species across the same time period. We correlated our range expansion simulations with the genetic patterns of the Egyptian mongoose (previously gathered in Barros et al. 2016a; Barros et al. 2016b) with the objective of assessing the relationship between genetic structure, range expansion, and landscape structure. Since landscape structure influenced the expansion of the Egyptian mongoose in Portugal (Barros et al. 2015, 2016a), we hypothesize that incorporating landscape resistance into range expansion models will improve the match with observed pattern of range expansion and genetic diversity. As allelic richness and heterozygosity are typically reduced at recently colonized areas compared with historical areas, we expect to find a positive correlation between simulated range expansion across a resistance surface and both genetic diversity measures. Therefore, two core hypotheses are addressed: (1) range expansion simulated based on landscape resistance will outperform a null model of uniform expansion, given that it reflects the cost-weighted pattern of expected colonization, and (2) cumulative resistant kernel value will predict observed allelic richness, such that allelic richness will be lower on the leading edge and higher in the center of the expanding population (central-marginal hypothesis).

Methods

Genetic data

We used 167 genotypes previously published (Barros et al. 2016b), obtained by amplifying ten microsatellites (Rodrigues et al. 2009). Deviations from Hardy–Weinberg equilibrium (HWE) were tested using the exact test in GENEPOP, version 4.2.1 (Rousset 2008), with 100 batches and 1000 randomizations. We used ARLEQUIN, version 3.5.1.2 (Excoffier and Lischer 2010) for estimating pairwise linkage disequilibrium for each pair of loci, with 10,000 permutations. Number of alleles (NA), as well as observed (HO) and expected (HE) heterozygosity, were calculated using GENALEX, version 6.501 (Peakall and Smouse 2012). Information regarding the genetic diversity results can be viewed in Appendix A.

Initial source points

The study area comprised the entire Portuguese continental territory (ca. 92,270 km^2; 35°570′ and 42°100′ N, and 6°120′ and 9°290′ E). It is believed that the Egyptian mongoose was confined to the southern Iberian Peninsula until recently (Delibes 1982) and started a rapid and sudden expansion at the end of the twentieth century. Hence, we modeled contagious range expansion from multiple source points in southern Portugal that reflect its range prior to the 1980s. To better reflect the putative original site from where the species expanded, the initial source area was calibrated with previous studies of the distribution of the species in the 1980s, before it started to expand (Barros 2009; Barros and Fonseca 2011; Barros et al. 2015). Based on previous information regarding the home range and territory size of the Egyptian mongoose (Palomares and Delibes 1991; Palomares 1993; Palomares and Delibes 1993a; Palomares and Delibes 1998), we initiated the simulation with a total 1634 of source points on the resistance map across southern Portugal, set uniformly on a grid and separated by 5 km of each other (Fig. 1).

Dispersal from initial source across resistance map

Middle elevations and dense shrub areas are the landscape features that most strongly influence genetic differentiation of the species in Portugal (Barros et al. 2016a). We applied this resistance model to decadal time steps across the extent of continental Portugal. Digital elevation data were gathered from the shuttle radar topography mission (http://srtm.usgs.gov/index.php). To model the resistance surface for each decade, vegetation cover for 1980s, 1990s, and 2000–2010 was retrieved from Corine Land Cover CLC90, CLC2000, and CLC2012 (http://www.eea.europa.eu/publications/COR0-land-cover), respectively. Raster maps were resampled to 250-m pixel size in ArcMap version 10.4 (ESRI). We modeled the resistance of each variable for each unit across three levels for altitude and vegetation cover. Landscape resistance of elevation was modeled as an inverted Gaussian function (Cushman et al. 2006), assuming a minimum of 1 and a maximum approaching an asymptote of 10, with a standard deviation of the Gaussian function of 5°. We modeled elevation according to the Barros et al. (2016a) results, in which elevation was considered to have the lowest resistance (1) at 1000 m. Levels of resistance for vegetation cover were modeled assuming a minimum resistance value of (1) in areas with high vegetation cover (see Barros et al. 2016a). Elevation and vegetation cover were modeled with equal weight using the fuzzy overlay tool.

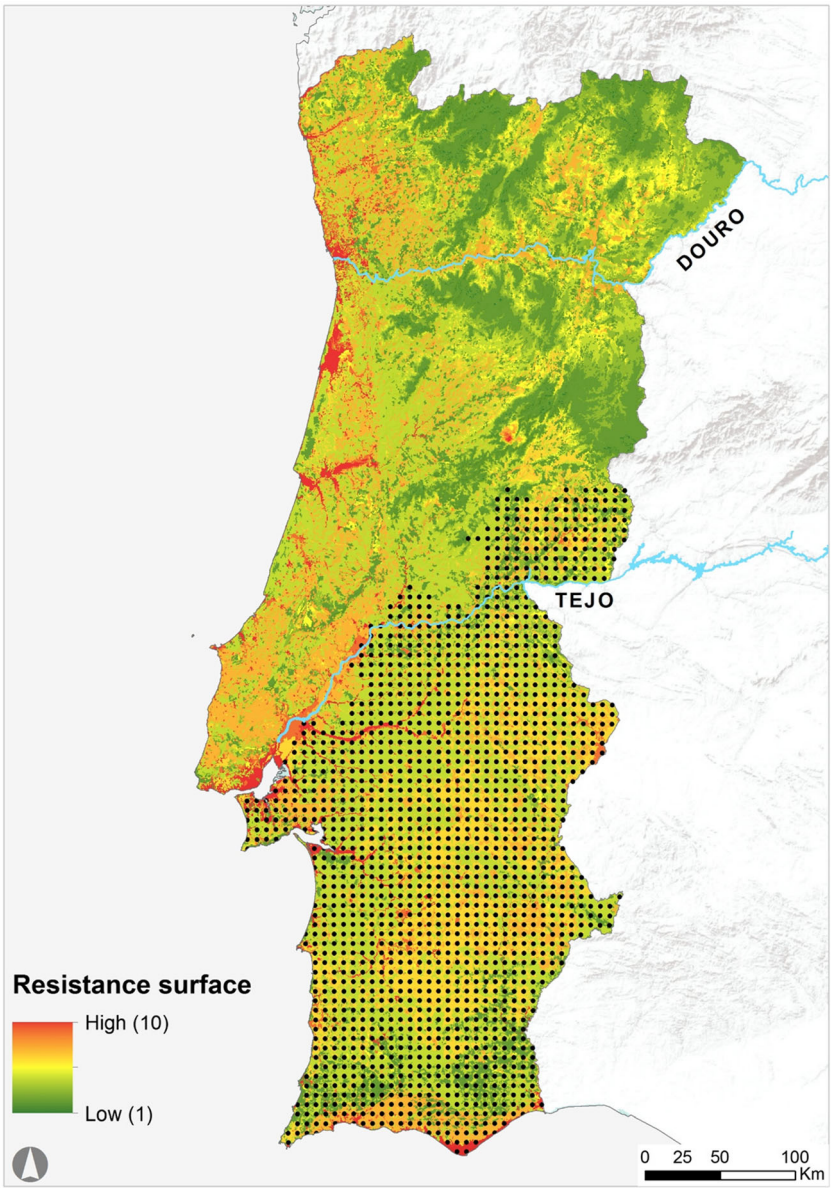

Fig. 1 initial source area of the expansion Egyptian mongoose selected for kernel resistant modeling. The source points are represented by black dots across a landscape resistance map showing elevation and vegetation cover

Resistant kernel analysis and correlation with genetic patterns

We followed Cushman (2015) approach for simulating range expansion with resistant kernel connectivity modeling. Kernel resistance modeling was performed with UNICOR (Landguth et al. 2012) which enables simulations of different movement patterns through a landscape matrix by using different dispersal functions and connectivity thresholds (Landguth et al. 2012). Through a modified Dijkstra's algorithm (Dijkstra 1959), every pixel is considered to be a node. According to Landguth et al. (2012), the graph edges representing possible movement paths between each node are weighted by the resistance value of the cell times the distance to the next pixel center, giving the total edge length in raster cell units (cost distance). Dijkstra's algorithm is modified in the UNICOR resistant kernel code to find all shortest paths (i.e., movement paths) to all destination nodes associated with the same starting node. This produces a kernel density estimate for each dispersal point which reflects the probability of the disperser being found in each cell in the landscape. The cumulative resistant kernel surface is the sum of all the individual dispersal kernels from the set of source cells and reflects the spatial incidence function of the full population of dispersers (e.g., Kaszta et al. 2018) and is proportional to the density of dispersers across the landscape. Population expansion from the putative initial colonization area was modeled on a yearly basis across a 30-year period using the resistant kernel functionality. The resistant kernel method calculated the expected relative density of dispersing Egyptian mongoose in each

pixel around the source given the dispersal ability of the species, the nature of the dispersal function, and the resistance of the landscape.

We produced two different resistant kernel simulations of range expansion. The first modeled range expansion as a function of landscape resistance (Barros et al. 2016b), and the second utilized a uniform resistance model, such that range expansion spreads contagiously from previously occupied areas, but is not affected by patterns of landscape resistance (null model). For the null model, landscape resistance was kept at a mean value of 2 uniformly across the landscape and we applied the same dispersal ability as in the resistance model (20,000 cost units). In both dispersal simulations, we evaluated dispersal abilities of 10,000, 20,000 and 30,000 cost units. These correspond to dispersal abilities of up to 10, 20, and 30 km, respectively, through continuously ideal habitat (high shrub cover at middle elevations; Barros et al. 2016a) for the resistance model, and all areas for the null model. In each year of the simulation, both resistance and null models produced predictions of kernel density, which reflects the expected frequency of dispersing mongooses moving through each cell in the landscape.

For simulating the dispersal and modeling the species establishment in each time step, we transformed the cumulative resistant surface into a binary (1 predicted present, 0 predicted absent) and multiplied this predicted occurrence kernel map from each year with a habitat suitability surface, which was calculated by inverting our landscape resistance surface and rescaling between 0 and 1. The rationale for this is that the kernel model may predict spread to locations that are unsuitable for establishment, and by multiplying by a suitability layer, only areas with high suitability are predicted to support the establishment of the spreading population. We multiplied this product with a random raster constituted by 0 and 1 values with an average of 0.5, in order to reflect the probabilistic but stochastic nature of establishment given dispersal to a suitable location. The establishment locations were selected as those that with a value greater than 1 in this product and resampled such that points were located every 5 km within areas meeting the establishment threshold. We defined the source points for each one of the following time-steps by taking those new establishment areas and adding them to the occupied cells predicted by the resistant kernel and site establishment steps. The combined set of source points was used as an input for the resistant kernel modeling for the subsequent time step. We used this iterative simulation to model the simulated pattern of population expansion across a 30-year period.

For comparison purposes, we intersected predicted (UNICOR) and observed (Barros et al. 2015) distribution on the mentioned three time steps by quantifying the difference between the resistance model and the null (isolation by distance—IBD—spread) model, and which had a higher match to the observed. With the aim of assessing the similarities between the observed expansion of the species with the outputs of UNICOR analysis (predicted), we calculated the percentage of intersected occupied area between the predicted occupied area overlapping observed occupied area for both the resistance and the null spread model for the three time steps.

We modeled mongoose expansion from 1980 to 2010 for both resistance and the null model. We compared the UNICOR results for these three time periods with previously published data regarding the distribution and evolution of the species expansion in 1990, 2000, and 2010 (Barros 2009; Barros et al. 2015). Given dispersal ability equivalent to 20,000 cost units in those three time steps, we carried out the full analysis using this value as the edge distance in UNICOR, which corresponds to the resistance distance threshold of kernel width in cost units. The selection of this edge distance value was also based on previous studies regarding the expansion of medium-sized carnivores (e.g., Rodrigues et al. 2014).

To test hypotheses 1 and 2 related to the central-marginal hypothesis—which can be linked with the cumulative kernel values and allelic surfing—we computed the following correlations: number of alleles, observed heterozygosity, and expected heterozygosity with (1) the cumulative kernel values for 1990, 2000, and 2010 for both resistance and null model, (2) the number of years that it took to reach the location where the genotypes were sampled through the resistance and null simulated models. To combine effects of time since colonization and core population effect, we correlated number of alleles and heterozygosity with the product of cumulative kernel values and years since colonization for both models. We calculated Spearman correlation for both resistance and null model in R (R Core Team 2013).

Results

The expansion of the Egyptian mongoose predicted by resistant kernel modeling was gradual, characterized by the presence of core areas of expected higher density of individuals, especially in the south and proximate to the northern edge of expansion during the first decade, within a broader area of predicted lower population density (see Appendix B). Given dispersal ability of 20,000 cost units and the resistance of the landscape at each time step, those core areas are constituted by cells with higher expected density from where simulated individuals disperse to the surrounding pixels (e.g., Compton et al. 2007; Cushman et al. 2010).

The main pattern of expansion through the resistance surfaces as a function of shrub areas and elevation was towards the countryside/east of the study area following a northward orientation, with the appearance of new core areas in the center and in the north of the territory during the second and third decades (see Appendix B). In the last time period (2010), our results show that the species is predicted to have spread across

the majority of the territory, albeit absent from coastal areas in the center and from the most northern regions (Fig. 2).

The null model shows a smoother expansion, with a continuous and homogenous spread during the considered time period. The final time step predicted occupation of all southern and central areas of Portugal, except the most northern regions (Fig. 2). The null model shows greater occupied area in all years, while the resistance model shows a slower increase of the occupied area, with a major peak between 1980 and 1981. The larger discrepancy between both models was found in 2003 (Fig. 3).

Intersections between both predicted distributional models (null and resistance) and the observed distribution of the species show that the percentage of overlapping area between the distribution predicted by the null model and the observed distribution of the species is higher in all three time steps compared with the area of intersection between the landscape resistance model and the observed distribution (Table 1). Spearman correlation for all tests using genetic data were not significant at the alpha 0.05 level. However, for the correlation between the number of alleles of each genotype and the number of years that each genotype location took to be occupied was positive and marginally significant for the null model (0.1443623; p value = 0.06) (see Appendix C).

Discussion

Understanding the spatial dynamics of range expansion through the combination of species distribution data and landscape resistance constitutes a major challenge for ecology and invasion biology. Previous studies showed that resistant kernel modeling provides a clearer and synoptic picture of the relation between environmental features and species distributions (e.g., Moqanaki and Cushman 2016; Puyravaud et al. 2016). If connectivity emerges from the interaction between landscape structure and spatiotemporal variation in dispersal (Baguette et al. 2013), then the application of such approaches in studies of range shift through time is even more important (e.g., Cushman 2015). Very few studies have applied resistant kernel functionality to simulate dispersal and expanding events through a landscape surface. Given that species dispersal is contingent upon landscape structure and dynamics (Baguette et al. 2013), it is expected that landscape structure and resistance to dispersal will affect the range expansion of a species, and methods which explicitly incorporate landscape resistance into simulations of range expansion (e.g., Cushman 2015) should outperform methods that do not incorporate landscape resistance.

Empirical observation showed progressive and accelerating range expansion for the Egyptian mongoose from 1980 to 2010. This is coincident with both rapid land use changes in shrub areas and warming climate, both of which are known to affect both distribution and genetic connectivity of the Egyptian mongoose population in Portugal (Barros et al. 2015; Barros et al. 2016a). Across the three studied decades, changes in vegetation cover were observed that had strong influence on landscape resistance (Barros et al. 2016a), which converges with the ecology of the species (Palomares and Delibes 1993a, 1993b, 1998).

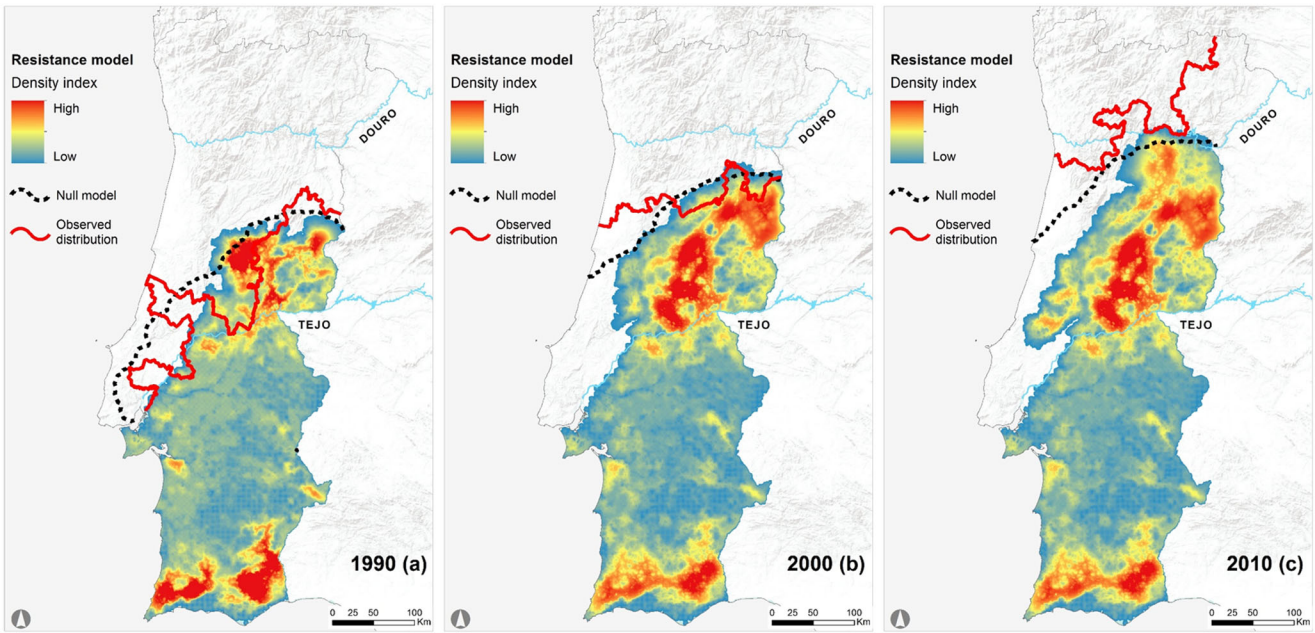

Fig. 2 Comparison of the density index of the resistance model, null model, and observed expansion of the Egyptian mongoose across the studied area in 1990 (**a**), 2000 (**b**), and 2010 (c) time steps. The lines represent the edge of the distribution of the species for each year given by the null and the resistance model

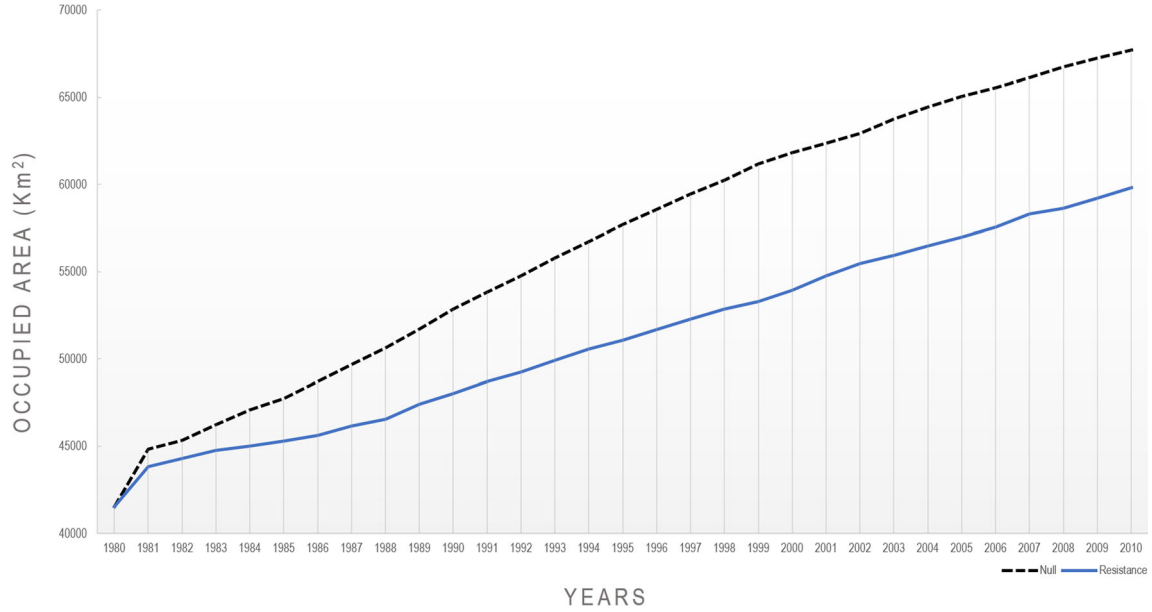

Fig. 3 Graph comparing the occupied area by the species in the resistance and null models simulated through resistant kernel modeling. Units are in square kilometers (km^2)

Our results show relatively high intersection of both the null and resistance models with the observed distribution of the species (Table 1; Fig. 2). Both the null model and the landscape resistance model underestimated the spread of the species, suggesting the possibility that the actual dispersal distance of the Egyptian mongoose is larger than that simulated. The landscape resistance model accounts for changes in landscape resistance across the studied area across the 30-year simulation time, while the null model includes a mean resistance value and all environmental areas assume to have the same influence in the presence or absence of the species (e.g., urbanized areas which are known to be avoided by the species; Palomares and Delibes 1993b). It is important to note that the observed distribution of the species is based on presence/pseudo-absence data collected from field observations, hunting records, road kills, and other sources (Barros et al. 2015), which may not truly reflect the distribution and ecological patterns of the species (see White et al. 2005; Shumway and Seabrook 2015). Additionally, dispersal distances show a frequency distribution characterized by long right tails, which reflects small proportions of individuals following long-distance dispersal events (see Nichols and Hewitt 1994). Due to the fact that dispersal distances have been modeled as a single value, this could partially explain the underestimation of the spread of the species and its gene flow, thus overlooking the existence of occasional long distance events.

Table 1 Percentage of the intersected areas between the observed occupied area and the predicted occupied areas for both null and resistance models

	Years		
Intersections between models	1990	2000	2010
POA/OOA	93%	84%	77%
POA_N/OOA	97%	96%	87%

OOA observed occupied area, *OUA* observed unoccupied area, *POA* predicted occupied area for the resistance model, *POA_N* predicted occupied area for the null model

By comparing the simulated expansion with what is known about the evolution of the distribution of the Egyptian mongoose (Barros and Fonseca 2011; Barros et al. 2015), we observe significant differences. For instance, Barros et al. (2015) recorded the presence of the species across the entire south, central, and north-western area of the Portuguese territory. Our results predicted absence of dispersal in a few western and north-western and north-eastern areas (Fig. 2). On the other hand, we did not find a significant correlation between the expansion and the number of alleles and heterozygosity of the species for both null and resistance models. The areas of high predicted population density from the resistant kernel model overlap areas of high relative shrub cover at middle elevation, which is consistent with the expectation that population density will be highest in areas with high connectivity and low resistance (e.g., Macdonald et al. 2018.

Hypothesis 1 was not supported through our results. The pattern of range expansion was better predicted by the null model than the landscape resistance model. In expanding populations, genetic patterns may be influenced by intrinsic factors, including the dispersal ability (Clobert et al. 2001; Chambers and Garant 2010) and also by environmental factors. However, to disentangle those factors is a major task. Sequential, stepwise range expansion generally results in a decrease of the genetic diversity in the population along the

expanding edge (Estoup et al. 2004; Short and Petren 2011), but the genetic outcomes of a range expansion are complex (Zenger et al. 2003), where local factors including migration events and the dynamics of the wave front are capable of affecting the genetic patterns of expanding populations (Excoffier et al. 2009). If long distance dispersal occurs through single colonizers that generate genetic structuring, populations may have low and altered diversity as a result of local founder effects (Nichols and Hewitt 1994; Bialozyt et al. 2006). In fact, microsatellite genetic patterns and mitochondrial DNA data of the Egyptian mongoose showed the possibility of long dispersal migrants from southern towards central and northern locations (Barros et al. 2016b; Barros et al. 2016c). If several dispersal events occurred, possibly from different locations, genetic diversity may increase with the expansion event (Brown and Stepien 2008; Parisod and Bonvin 2008; Darling and Folino-Rorem 2009; Bronnenhuber et al. 2011), which hinders the correlation between genetic patterns and expansion.

Following Bothwell et al. (2017) and MacDonald et al. (2018), we expected to find significant correlations between cumulative resistant kernel value, which reflects the degree of centrality in the population and is proportional to expected rates of local gene flow, and allelic richness (hypothesis 2). Contrary to our hypothesis 2, allelic richness in the mongoose population at year 2010 was most correlated with time since simulated colonization in the null model, and not associated with time since colonization in the resistance model, and not significantly associated with cumulative resistant kernel value in either the landscape resistance or null model. These results might indicate an allelic surfing of reduced genetic diversity on the leading edge of the population, where the population is expanding according to the null model, and not the resistance model. In contrast, we found no support for the central-marginal hypothesis expectation of higher genetic diversity in the core areas with high rates of internal gene flow (Bothwell et al. 2017; MacDonald et al. 2018), given we found no correlation between allelic richness and cumulative kernel value, or the combination of time since colonization and the cumulative kernel value. This suggests that range expansion of the Egyptian mongoose and its genetic diversity may not be well predicted by landscape resistance models developed through association of observed genetic differentiation with landscape features.

Our results complement what is known about the expansion and distribution of the Egyptian mongoose in Portugal by providing a dynamic simulation of several scenarios of range expansion across 30 years. Our results show that the interaction between range expansion, landscape resistance, and genetic diversity are not straightforward, and that direct application of iterative resistant kernel modeling on empirically derived resistance surfaces may not provide an improved understanding of prediction over simple, uniform null models.

This study is the first to test predictions of resistant kernel range expansion simulation with empirical data on actual patterns of a complex range expansion and genetic diversity of a real population. The implications of our study are concentrated on two axes: (1) a local and ecological relevance axis, in which our synoptic dynamic predictive modeling provides an improved picture of the expansion of the Egyptian mongoose in the Portuguese territory, and (2) a global and theoretical relevance axis, where our study stresses the application of dynamic modeling of range expansion in resistant landscapes.

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