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# Human-aided and natural dispersal drive gene flow across the range of an invasive mosquito

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## Abstract

Human-aided transport is responsible for many contemporary species introductions, yet the contribution of human-aided transport to dispersal within non-native regions is less clear. Understanding dispersal dynamics for invasive species can streamline mitigation efforts by targeting routes that contribute disproportionately to spread. Because of its limited natural dispersal ability, rapid spread of the Asian tiger mosquito (*Aedes albopictus*) has been attributed to human-aided transport, but until now, the relative roles of human-aided and natural movement have not been rigorously evaluated. Here, we use landscape genetics and information-theoretic model selection to evaluate 52 models representing 9240 pairwise dispersal paths among sites across the US range for *Ae. albopictus* and show that recent gene flow reflects a combination of natural and human-aided dispersal. Highways and water availability facilitate dispersal at a broad spatial scale, but gene flow is hindered by forests at the current distributional limit (range edge) and by agriculture among sites within the mosquito's native climatic niche (range core). Our results show that highways are important to genetic structure between range-edge and range-core pairs, suggesting a role for human-aided mosquito transport to the range edge. In contrast, natural dispersal is dominant at smaller spatial scales, reflecting a shifting dominance to natural movement two decades after introduction. These conclusions highlight the importance of (i) early intervention for species introductions, particularly those with readily dispersed dormant stages and short generation times, and (ii) strict monitoring of commercial shipments for transported immature stages of *Ae. albopictus*, particularly towards the northern edge of the US range.

**Keywords:** *Ae. albopictus*, chikungunya, disease vector, exotic species, landscape genetics

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## Introduction

Since the inception of long-distance travel, humans have introduced exotic species to new regions (Randolph & Rogers 2010). Introductions of disease vectors have led to outbreaks of severe and potentially fatal diseases such as plague, malaria and, more recently, chikungunya (Lounibos 2002; Reiter *et al.* 2006; Charrel *et al.* 2007). While the contribution of human-aided transport to species introductions is well understood, the relative influence of anthropogenic factors and natu-

ral dispersal to 'range filling' after a species becomes invasive is much less clear (Kolar & Lodge 2001; Shigesada & Kawasaki 2001). Yet, human-aided dispersal may contribute substantially to spread so that identifying important dispersal corridors has great potential for mitigating invasion and disease risk. Moreover, because dispersal is linked to gene flow (Bohonak & Jenkins 2003), human-altered dispersal patterns during invasion could influence genetic structure and long-term evolutionary trajectories (Slatkin 1985; Vellend *et al.* 2007; Suarez & Tsutsui 2008), potentially altering mitigation efforts and the effects of invaders on native ecosystems.

A global invader with a history of human-aided transport and important human health implications is

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the Asian tiger mosquito, *Aedes albopictus* (Skuse). This mosquito breeds in natural and artificial containers such as treeholes, used tires and cemetery vases. Native to South-East Asia, *Ae. albopictus* has invaded North and South America, Europe and Africa since the late-1800s (Lounibos 2002). *Ae. albopictus* is a vector for numerous diseases worldwide, including chikungunya (Reiter *et al.* 2006), and several viruses have been isolated from wild-caught adults in the USA (Gratz 2004). After its putative US introduction in Houston, TX, in 1985 via used tires (Hawley *et al.* 1987), it rapidly expanded: by 1986, it had already spread across 12 degrees latitude and has since coalesced into one large US range (Medley 2010). Because of its limited natural dispersal capacity (Liew & Curtis 2004), long-distance transport facilitated by commercial shipping (used tires, lucky bamboo plants) and private automobiles was implicated in its rapid spread (Lounibos 2002). Continued human-aided transport within the invaded range may facilitate long-distance dispersal events and aid in recolonization of sites that have been locally eradicated. Thus, identifying corridors for spread is an important goal for streamlining mitigation efforts and for preventing disease outbreaks in human and wildlife populations in the USA and across the globe. Moreover, lessons learned with *Ae. albopictus* spread may be relevant to other exotic species with similar life histories.

The detection of dispersal pathways is now possible through the integration of population genetics, landscape ecology and geospatial statistics into the subdisciplines of landscape genetics and genomics (Manel *et al.* 2003; Storfer *et al.* 2007, 2010; Andrew *et al.* 2013). Taxonomic foci of such studies have been generally biased towards vertebrates (Storfer *et al.* 2010), particularly amphibians (Murphy *et al.* 2010; Spear & Storfer 2010). This is for good reason; many amphibians are of conservation concern and have relatively low vagility, leading to marked population genetic structure and strong effects of landscape (Murphy *et al.* 2010; May *et al.* 2011; Hether & Hoffman 2012). In contrast, species with higher mobility such as flying insects or those affected by human-aided dispersal (i.e. with inflated dispersal distances and/or rates) are more difficult to study because genetic structure is often less pronounced. However, genetic structure need not be marked to detect relationships between landscape and genetic distance. Moreover, the relationship between landscape features and flight has not been well studied to date (Rasic & Keyghobadi 2012), but is an area with great potential. For instance, three-dimensional habitat can affect flight ability between localities by providing refuge from predators and wind. Moreover, stepping-stone dispersal between proximal sites is more likely to occur where habitat is suitable and correlations between

suitable habitat and genetic distance should reveal such behaviour. We extend the landscape genetics approach to include models representing human-aided dispersal routes to evaluate the relative roles of natural and human-altered movement to gene flow of *Ae. albopictus* in the USA. Anthropogenic alterations to the landscape and subsequent effects on connectivity and gene flow for natural populations are commonly addressed themes within landscape genetics (Lada *et al.* 2008; Radespiel *et al.* 2008; Spear & Storfer 2010; Storfer *et al.* 2010). However, few landscape genetics studies have addressed species invasions (Zalewski *et al.* 2009), and to our knowledge, none have explicitly used this approach to detect human-aided dispersal (i.e. highway dispersal).

Knowledge of the invasion history and dispersal ability of invasive species can inform predictions about their likely dispersal routes and potential for spread. Natural dispersal (e.g. flight) by *Ae. albopictus* is relatively limited, as evidenced by adults dispersing  $\leq 1$  km from natal habitat in a lifetime (Liew & Curtis 2004), and high genetic differentiation among populations previously revealed within and outside the USA (Black *et al.* 1988, 1989; Kambhampati *et al.* 1990; Urbanelli *et al.* 2000; Ayres *et al.* 2002). Such movement likely occurs where suitable habitats are widely available; *Ae. albopictus* females oviposit in fishless water bodies and artificial containers, so natural dispersal should be high among sites where water availability is sufficient to maintain dense breeding habitat. Forests may facilitate dispersal because adult *Ae. albopictus* rest along forest edges near breeding sites (Hawley 1988). However, larvae have been detected in commercial shipments, and adults can travel in motorized vehicles (Lounibos 2002; Enserink 2008), providing evidence that dispersal is markedly enhanced by commercial transport along highways. The rapid expansion of *Ae. albopictus* after its initial establishment in the USA also suggests an important role for human-aided transport to the movement of this species. In addition, the current US range for *Ae. albopictus* has expanded beyond climatic predictions based on its native distribution (Medley 2010), and identifying potential corridors for the expansion should inform future work evaluating causation.

Here, we use landscape genetics and information-theoretic model selection to address three key questions across the US range of *Ae. albopictus*: (i) What is the dominant dispersal mode (i.e. human-aided or natural) across the range? (ii) What are the dominant land-cover types influencing dispersal and gene flow between US cities? and (iii) which dispersal mode (human-aided or natural) and land-cover type(s) are most likely responsible for the northward expansion of *Ae. albopictus* beyond its native climatic niche (*sensu* Medley 2010)?

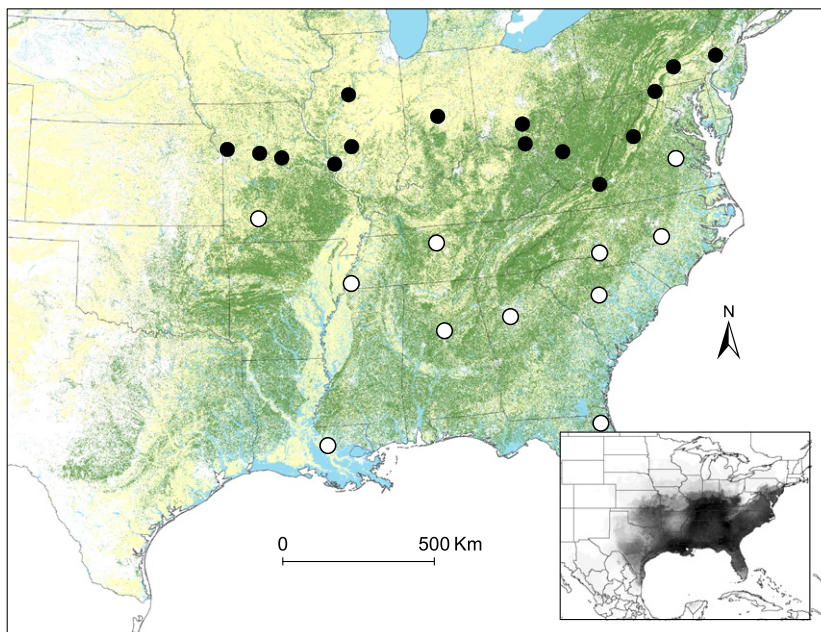
To address questions 1 and 2, we compare among 52 dispersal models (9240 pairwise dispersal pathways) representing human-aided transport via highways (weighted by traffic volume) and natural dispersal across vegetated and urban lands and water bodies. To evaluate question 3, we also tested our dispersal models using three reduced data sets: among sites along the northern range edge, among sites deeper within the range core and between pairs of range-core and range-edge sites (see Fig. 1). We expected this partitioned analytical approach to reveal differential dispersal modes that could explain northward expansion of *Ae. albopictus*, and to inform future tests on the relationship between gene flow and adaptation to northern climate. Finally, we simultaneously evaluated the performance of two landscape distance metrics (least-cost paths and resistance distances) relative to classic isolation by distance (Jenkins *et al.* 2010) and compared two genetic distance measures for their sensitivity to detect pattern at broad spatial scales. Together, our analyses provide a comprehensive evaluation of recent movement across the US range for *Ae. albopictus* and provide a comparative analysis among multiple approaches currently in use within the field of landscape genetics.

## Methods

### *Study species and sampling*

The Asian tiger mosquito (*Ae. albopictus*, Diptera: Culicidae) is a container mosquito whose females lay eggs singly in treeholes and artificial containers just above

water line. After rains, eggs become inundated and hatch into larvae that undergo 4 instars prior to a pupal stage. *Ae. albopictus* opportunistically colonizes artificial containers (e.g. cemetery vases, discarded tires) and readily outcompetes other larvae in most environments (Braks *et al.* 2004; Bevins 2007). Females lay eggs in multiple containers, and multiple females lay eggs in the same container (Hawley 1988). Thus, a single container can potentially contain offspring from a wide selection of individuals from the local population. We collected larvae and pupae from *c.* 20 abandoned flower vases (>100 individuals per site) in cemeteries from 26 localities at the edge and within the core of the US range (Fig. 1, Table 1). We defined range edge and range core based on the current distribution for *Ae. albopictus* and the extent to which climate at sites was within the native climatic niche for *Ae. albopictus*. Range-edge sites were located along the northern edge of the current distribution and at sites that were approaching or beyond the native climatic niche (Medley 2010). Range-core sites were located at least 160 km from the current range edge and at sites that were well within the native climatic niche for *Ae. albopictus* (Medley 2010). To capture gene flow across a wide range of land-cover types, we collected from cemeteries in larger cities surrounded by urban land cover (e.g. St. Louis, MO, USA; Indianapolis, IN, USA) and from cemeteries in rural areas and smaller towns (e.g. Marshall, MO, USA; Charleston, WV, USA) that were typically bordered by forests and agricultural landscapes. All cemeteries contained trees and/or were surrounded by patches or broader swaths of wooded areas to varying



**Fig. 1** Sample localities in 26 US cities within the US range for *Ae. albopictus*. Range-edge localities in black, range-core localities in white, water bodies in blue, forests in green and agriculture in yellow. Inset: approximate range of *Ae. albopictus*.



**Table 1** Geographic coordinates (decimal degrees), range location (region) and sample size for all sampling localities. See Figure 1 for position of range core and range edge

Locality	Region	Latitude	Longitude	<i>n</i>
Atlanta, GA	Core	33.75	-84.45	29
Baton Rouge, LA*	Core	30.46	-91.14	31
Birmingham, AL	Core	33.55	-86.75	31
Charlotte, NC	Core	35.23	-80.84	31
Columbia, SC	Core	33.97	-80.95	31
Jacksonville, FL	Core	30.37	-81.65	31
Memphis, TN	Core	35.12	-90.03	30
Nashville, TN	Core	36.15	-86.73	31
Raleigh, NC	Core	35.79	-78.63	31
Richmond, VA	Core	37.54	-77.40	28
Springfield, MO*	Core	37.19	-93.28	30
Blacksburg, VA	Edge	38.35	-81.61	22
Charleston, WV	Edge	38.35	-81.64	31
Chillicothe, OH	Edge	39.32	-82.99	31
Columbia, MO*	Edge	38.95	-92.34	31
Doylestown, PA	Edge	40.32	-75.13	29
Hagerstown, MD	Edge	39.63	-77.72	31
Harrisburg, PA	Edge	40.27	-76.87	31
Harrisonburg, VA	Edge	38.43	-78.85	22
Indianapolis, IN	Edge	39.77	-86.15	31
Liberty, MO*	Edge	39.23	-94.42	31
Litchfield, IL	Edge	39.17	-89.63	31
Marshall, MO	Edge	39.10	-93.17	31
Portsmouth, OH	Edge	38.73	-82.97	30
St. Louis, MO	Edge	38.64	-90.29	22
West Peoria, IL	Edge	40.70	-89.62	31

\*Sites that were removed from model selection because pairwise genetic distances for the site were not independent.

degrees, even those in urban areas. This design also allowed for capturing a range of gene flow estimates, because larger cities likely have larger mosquito populations (e.g. more artificial containers and sources of bloodmeals) and are more important source populations for dispersal than are smaller towns.

#### Laboratory husbandry

To ensure the species identity of field-collected pupae and larvae, we reared immature stages to adults under laboratory conditions in black plastic cups (*c.* 300 mL) at a density of *c.* 50 individuals per cup. Cups were placed in 30 × 30 cm mesh cages under a long-day photoperiod (18:6 L/D) and fed a combination of ground fish food and cultured infusorium from leaves (*Quercus* spp., *Platanus* spp.) incubated in water for 7 days. Culture cups were filled with infusorium water and leaves. After emergence from pupae, we killed adults by exposing them to freezing temperatures for *c.* 30 min and preserved them in 99% ethanol.

#### DNA extraction and genotyping

We extracted DNA from 1 to 2 legs per adult mosquito using a chelex extraction protocol (Walsh *et al.* 1991). We genotyped 739 individuals at nine polymorphic microsatellite loci: AealbA9, AealbB52, AealbD2, AealbF3, Ap1, Ap2, Ap3, Ap5 and AC2 (Behbahani *et al.* 2003; Porretta *et al.* 2006; Slotman *et al.* 2006). PCRs were conducted in a total volume of 20 μL, and the product was amplified under the following conditions: 94 °C for 3 min, 30 cycles of 30 s at 94 °C, 45 s at a locus-specific annealing temperature ranging from 48 °C to 60 °C, 45s at 72 °C and a final extension for 5 min at 72 °C. M-13 tails (5'-TGTAACGACGGCCAGT-3') were attached to forward primers for fluorescent labelling (Schuelke 2000). We used Microchecker v2.2.3 (Van Oosterhout *et al.* 2004) to screen for high-frequency null alleles (>0.08), allelic dropout and scoring errors and tested for pairwise linkage disequilibria and significant deviations from HWE using Fisher's exact tests with GENEPOP v4.0.7 (Raymond & Rousset 1995). We detected one locus (Ap2) with high-frequency null alleles and excluded it from reported analyses. Five comparisons were significantly out of Hardy-Weinberg equilibrium (HWE), but no locality had more than one locus out of HWE.

#### Landscape genetics

**Genetic distance.** We measured two types of genetic distance shown to perform well in landscape genetic studies (Garroway *et al.* 2011; Hether & Hoffman 2012): Dps' and cGD. We measured Dps' (Bowcock *et al.* 1994; hereafter Dps) as (1-*P<sub>s</sub>*), where *P<sub>s</sub>* is the number of shared alleles summed over loci/(2 × number of loci compared), using MICROSAT v 1.5b (Bowcock *et al.* 1994; Minch *et al.* 1996). We measured cGD as the shortest graph distance between locality pairs using the Graph function in GENETICSTUDIO (Dyer 2009).

**Landscape distance.** We measured landscape distances among all pairs of sites using GIS-based least-cost path analysis and electrical circuit theory (McRae *et al.* 2008). Both approaches differ from straight-line, isolation-by-distance theory because they account for habitat configuration between pairs of sites.

Least-cost path models correlate genetic distance with landscape distance along the shortest, single suitable path between localities (Vignieri 2005). Circuit models measure resistance distances between sites by allowing multiple pairwise connections, where broader swaths of suitable habitat facilitate higher rates of gene flow (McRae & Beier 2007). For both techniques, we measured landscape distances across 19 individual land-cover types and four combined land-cover types

**Table 2** Land-cover types used to model natural and human-influenced dispersal pathways. Natural pathways represent dispersal across naturally occurring land-cover types (water, forests, scrub, grassland). Human-influenced pathways include dispersal via highways and across human-dominated landscapes (farms and urban areas). Detailed definitions of land-cover types can be accessed via [www.mrlc.gov/nlcd11\\_leg.php](http://www.mrlc.gov/nlcd11_leg.php)

Natural	Human-influenced dispersal
Water	Highways
Woody wetlands	Farm
Herbaceous wetlands	Pasture/hay
Open water	Cultivated crops
All water*	All farm <sup>†</sup>
Forest	Urban areas
Deciduous	Low intensity
Evergreen	Medium intensity
Mixed	High intensity
All forest	Developed open area
Scrub <sup>‡</sup>	All urban <sup>§</sup>
Grassland/herbaceous	

\*Dispersal pathways were modelled across all land-cover types in the 'water' category.

<sup>†</sup>Dispersal pathways were modelled across all land-cover types in the 'farm' category.

<sup>‡</sup>Includes dwarf scrub and scrub/shrub.

<sup>§</sup>Dispersal pathways were modelled across all land-cover types in the 'urban' category.

(Table 2). These included 10 land-cover types across which mosquitoes disperse naturally (e.g. flight, stepping-stone dispersal), such as wetlands and forest, and 9 land-cover types where human modification of the landscape has likely influenced mosquito movement by reducing the density of natural containers (e.g. pasture, crops) or increasing the density of artificial containers and bloodmeal sources (e.g. urban areas). The four combined models calculated distances across broader land-cover categories (all water, all forest, all farm, all urban; Table 2). Finally, we explicitly tested the role of human-aided transportation via commercial shipping and vehicles by measuring highway distances between pairs of sites, where shorter distances represent corridors with higher traffic volume.

To measure distances along pairwise connections among sites, we created landscape models using a 30-m-resolution land-cover data set (Fry *et al.* 2011) and the Spatial Analyst extension in ARCGIS 10. Land-cover data were resampled to a 1 km<sup>2</sup> grain size to improve computational efficiency at the broad study extent. The recommended grain size is equal to or smaller than the average dispersal distance for the focal species (Fortin & Dale 2005). Natural dispersal distances for *Ae. albopictus* individuals approximate *c.* 800–1000 m<sup>2</sup> (Liew & Curtis 2004), but many dispersal events occur over much broader spatial scales. Thus, we believe the

improvement of computational efficiency was a worthwhile trade-off to a smaller grain size.

Using the land-cover raster, we created a cost surface and a resistance surface for each landscape model. For least-cost surfaces, we assigned a low cost to the focal land-cover type from the landscape model and a high cost to all other land-cover types using the Spatial Analyst extension in ARCGIS 10. Costs were standardized across all models to values between 0 and 1 to ensure comparability. We measured the least-cost distance as the distance along the path that accrued the least cumulative cost between pairs of sites.

We calculated resistance distances from landscape surfaces based on a graph-theoretic framework using Circuitscape 3.5.4 (Shah & McRae 2008). Resistance surfaces assigned low resistance to the focal land-cover type and high resistance to all other types. Using Circuitscape, we generated pairwise paths and measured resistance distances from the resistance surfaces. We selected pairwise mode to iterate across all focal nodes (localities), the option for focal points containing a single cell (rather than a region), and selected an 8-neighbour cell-connection scheme.

In total, we calculated 160 550 pairwise landscape distances (325 pairwise distances over 494 cost-distance surfaces).

#### Model selection and parameter estimation

We modelled landscape effects on genetic distance using an information-theoretic model-selection framework (Burnham & Anderson 2001) to select the most plausible model(s) explaining genetic distance (Dps and cGD). Landscape genetics often uses Mantel tests to correlate pairwise genetic distance with geographic distance (Storfer *et al.* 2010), which are generally limited to three matrix comparisons (one response matrix and two predictor matrices). Multiple regression on two predictor matrices (MRDM; Legendre & Legendre 1998; Lichstein 2006) provides a framework to evaluate effects of multiple predictors on pairwise genetic distance, to calculate the coefficient of determination (R<sup>2</sup>) for each predictor and to evaluate the relative importance of each predictor variable on genetic distance. Moreover, this approach has high power and little type I error compared to commonly used Mantel and partial Mantel tests (Balkenhol & Waits 2009). Thus, the relative role of multiple landscape characteristics can be objectively assessed using this approach.

We used MRDM to fit 26 models to two genetic distances (52 models total) representing human-aided and natural dispersal across multiple land-cover types. Because each sample site has multiple genetic distances associated with it, we tested for autocorrelation of these

values using a simulation method modified from Delaunay triangulation (Goldberg & Waits 2010). We detected autocorrelation by comparing the similarity between the mean rate of genetic distance for each site (genetic distance/landscape distance) and the mean rate of genetic distance sampled from a null distribution. To create the null distribution, we bootstrap resampled similarities of rates of genetic distance 10 000 times from a full matrix of similarities between rates of genetic distances from the entire data set. We compared the mean similarity from the empirical data to the null distribution; a  $P$ -value  $< 0.05$  (after Bonferroni correction) was considered nonindependent, and the site was removed from the analyses.

Landscape distances were included as models individually or in combination with other distances based upon highways (distance-weighted by traffic), and combinations of land-cover and highways (i.e. natural and human-aided dispersal; Table 2 & Table S2, Supporting information). We also included models representing simple isolation by distance (IBD, based on Euclidean distance only), a random model and a null model (response variable = 1). The model set also included two genetic distance measures, Dps and cGD. We evaluated collinearity among variables by creating a correlation matrix and calculating variance inflation factors (VIF; Burnham & Anderson 1998). Variables with a correlation coefficient  $< 0.5$  and a VIF  $< 1.1$  were not considered collinear and were included within additive models. We calculated model significance using 10 000 permutations of Dps. We considered the model with the lowest AIC value and the highest model weight as the most plausible model in the set. To compare subordinate models, we evaluated the evidence ratio as the weight of the top model divided by the weight of the model in the comparison. The evidence ratio for the top model is always one. If the evidence ratio for a lesser model is, for example, 3, the top model is three times better than the model in the comparison. We used the evidence ratio to compare the most plausible model to the next best model and to the null and IBD models. We considered top models equally important if their AIC value was within 2 AIC units; if the top model exceeded this difference, only one model was considered 'best' (Burnham & Anderson 1998). All statistical analyses were conducted in R using the base package (R Core Team 2013).

## Results

### Population genetics

Pairwise Dps ranged 0.11–0.28, and pairwise cGD ranged 0.02–0.11 (Table S1, Supporting information).

Conditional genetic distance (cGD) performed poorly in landscape models with a maximum  $R^2 = 0.04$ , whereas models using Dps performed consistently better ( $R^2$  ranged 0.10–0.25). Thus, we report landscape modelling results for models using Dps.

### Landscape distance

Landscape distance between pairs of locations can be modelled by least cost or resistance (McRae *et al.* 2008; Van Strien *et al.* 2012). For our model set, the top models at broad spatial scales (core-edge pairs, all pairs) were those that used least-cost distances. For comparisons within the range core or within the range edge, models using resistance distances provided a better fit (Table 3).

### Model selection

Our autocorrelation analyses revealed four sites whose genetic distances were not independent: Baton Rouge, LA; Columbia, MO, Liberty, MO, and Springfield, MO. Data from these sites were omitted from the analyses.

*All localities.* Among all 22 (independent) localities (Table 3, 231 pairwise comparisons), the most plausible model was the additive model including least-cost distance across all water bodies, forests and highways. This model performed substantially better than all other models in the model set with a weight of 0.90, where the second most plausible model had a weight of 0.03 (Table 3). This model was  $> 28$  times more informative than the next best model and over 19 000 times more informative than a model representing classic isolation by distance (IBD, Table 3). The relationship between distance across water bodies and genetic distance was positive and significant; as water body density increased, gene flow increased (Table 4). The relationship between highway distance and genetic distance was positive, but not significant across all sites (Table 4). Distance across forests, in contrast, was significantly negatively associated with genetic distance; as forest density increased, gene flow decreased (Table 4).

*Core-edge locality pairs.* To evaluate potential routes for northward range expansion, we compared landscape genetics models representing dispersal between range-core and range-edge localities (113 pairwise comparisons). Similar to the model selection for all localities, the most plausible model for core-edge pairs was the additive model including least-cost distance across all water bodies, forests and highways. This model was more informative than all other models in the model set

**Table 3** Two most informative models for genetic distance (Dps) between all locality pairs, core-edge pairs, range-edge localities and range-core localities. The most informative model was chosen as the model with the lowest AIC and the highest model weight. A null model (response = 1) and a model representing isolation by distance (IBD; geographic distance) are also provided for comparison of model performance. Model parameters are provided in Table 4

Model	d.f.	K	Log (ℓ)	AIC	w <sub>i</sub> *	Evidence <sup>†</sup>
All locality pairs ( <i>n</i> = 231)						
All water LCP + all forest LCP + highway LCP	227	4	490.6060	-971.02	0.90	1
All water LCP	229	2	482.36	-964.67	0.03	28.88
Null model	230	1	478.35	-952.69	0.00	9542
Geographic distance (log)	229	2	478.67	-952.34	0.00	19 192
Core-edge pairs ( <i>n</i> = 113)						
All water LCP + all forest LCP + highway LCP	109	4	241.83	-473.28	0.66	1
Highway LCP + geographic distance	110	3	237.97	-467.72	0.04	16.08
Null model	112	1	234.04	-464.07	0.01	101.53
Geographic distance	111	2	234.50	-462.89	0.0002	179.94
Edge locality pairs ( <i>n</i> = 78)						
All forest R	76	2	160.71	-315.43	0.33	1
Deciduous forest R	76	2	160.00	-313.83	0.16	2.05
Null model	77	1	154.92	-305.80	0.002	114.0
Geographic distance	76	2	156.12	-306.07	0.001	99.35
Core locality pairs ( <i>n</i> = 30)						
All farm R + geographic distance	27	3	74.83	-140.73	0.16	1
All farm R	28	2	73.02	-139.59	0.09	1.77
Null model	29	1	70.55	-136.96	0.03	6.59
Geographic distance	28	2	71.20	-135.96	0.02	10.87

d.f., degrees of freedom; K, number of parameters estimated; log (ℓ), maximized log likelihood; AIC, Akaike’s information criterion; R, resistance distance; LCP, distance along a least-cost path.

\*Model weight = probability that model is the actual (fitted) Kullback Leibler best model in the set.

†Evidence ratio = model weight of top model/model weight of candidate model.

**Table 4** Results for most informative model for genetic distance (Dps) between all pairs of localities, core-edge pairs, range-edge pairs and range-core pairs

Source	d.f.	Estimate	SE	<i>t</i>	<i>P</i>	<i>R</i> <sup>2</sup>
All locality pairs ( <i>n</i> = 231)						
Intercept		0.19	$6.26 \times 10^{-3}$	29.60	≪0.001	0.10
All water LCP	1	$6.34 \times 10^{-10}$	$1.72 \times 10^{-10}$	3.70	<0.0001	
All forest LCP	1	$-3.24 \times 10^{-9}$	$1.02 \times 10^{-9}$	-3.19	0.002	
Highway LCP	1	$5.66 \times 10^{-4}$	$3.54 \times 10^{-4}$	1.60	0.112	
Error	227	0.03				
Core-edge pairs ( <i>n</i> = 113)						
Intercept		0.18	$9.58 \times 10^{-3}$	18.38	≪0.001	0.13
All water LCP	1	$5.32 \times 10^{-10}$	$2.55 \times 10^{-10}$	2.09	0.04	
All forest LCP	1	$-3.17 \times 10^{-9}$	$1.40 \times 10^{-9}$	-2.26	0.03	
Highway LCP	1	$1.44 \times 10^{-3}$	$5.26 \times 10^{-4}$	2.74	0.007	
Error	109	0.03				
Edge pairs ( <i>n</i> = 78)						
Intercept		0.24	0.01	18.65	≪0.001	0.14
All forest R	1	$-1.78 \times 10^{-4}$	$5.12 \times 10^{-5}$	-3.49	0.001	
Error	76	0.03				
Core pairs ( <i>n</i> = 30)						
Intercept		0.15	0.03	5.40	≪0.001	0.25
All farm R	1	$1.86 \times 10^{-4}$	$6.86 \times 10^{-5}$	2.72	0.01	
Geographic distance	1	-0.04	0.02	-1.87	0.07	
Error	27	0.02				

LCP, distance along least-cost path; R, resistance distance.



with a weight of 0.66, where the second most informative model had a weight of 0.04 (Table 3). This model was >16 times more informative than the next best model and nearly 180 times more informative than a model representing classic isolation by distance (IBD, Table 3). The relationships between distances across water bodies and highway distance were positive and significant (Table 4). Gene flow between cities increased as water body density and high-volume highway connections increased (Table 4). In contrast, distances across forests were significantly negatively related to genetic distance; as forest density increased, gene flow decreased (Table 4).

*Range-edge localities.* Among range-edge localities (78 pairwise comparisons), the most plausible model was resistance distance across forests (including all forest types), with a model weight of 0.33 (Table 3). This was nearly 100 times more informative than IBD, but a second model representing resistance distance across deciduous forest was nearly equally supported with a model weight of 0.16 (Table 3). Genetic distance and resistance distance of all forests had a significant negative relationship; gene flow decreased as forest density increased (Table 4).

*Range-core localities.* Among range-core localities (30 pairwise comparisons), additive model with resistance distance across farms and straight-line geographic distance was the most plausible (Table 3) with a model weight of 0.16. This model was just over 10 times more informative than IBD and 6 times more informative than the null model, and a second model with farm resistance distance alone was nearly as informative with a model weight of 0.09 (Table 3). Compared to other analyses, those within the range core had the strongest evidence of isolation by distance because of the influence of straight-line distance to model fit. After accounting for this pattern, resistance distance across farms had a significant and negative relationship with genetic distance; farm density hinders gene flow in the range core (Table 4).

## Discussion

Using an integrative landscape genetics framework to compare among models representing competing hypotheses, we provide the first assessment of the relative contribution of human-aided vs. natural dispersal to recent movement for an invasive species. Because many introduced species including disease vectors and pathogens arrive in new regions via human transport (Crowl *et al.* 2008), their capacity for spread into climatically suitable areas may be high. Introduced species

may rapidly fill new ranges and become fully established in non-native regions, particularly if they possess traits such as easily transported dormant stages (e.g. eggs in diapause, dormant seeds), human-associated habitat requirements (e.g. containers, plantations) and short generation times. For instance, the red imported fire ant, *Solenopsis invicta*, arrived in the USA in the 1930s and is thought to disperse via automobiles, shipments of nursery stock and floodwaters (Tschinkel 2006). These modes of transport can be tested using landscape genetics, and particular sites on the landscape can be identified as important areas to focus mitigation. Many other invasive species may also be good candidates for this approach (e.g. Kudzu, emerald ash borers, zebra mussels).

For *Ae. albopictus*, we provided the first rigorous test of long-standing hypotheses about the spread of the Asian tiger mosquito in the USA. We explicitly tested the role of human-aided transport by including highway dispersal models – where high-traffic routes corresponded to shorter effective landscape distances – and models representing human-facilitated dispersal across urban and agricultural areas. Our spatially partitioned analyses show that gene flow for *Ae. albopictus* is influenced by a combination of human-aided and natural dispersal at the scale of the US range, and the role of human-aided dispersal via highways is more apparent between the core and edge of the range. However, agricultural land use inhibits mosquito dispersal between cities within the relatively smaller scale of the range core.

At the two broadest spatial scales (all localities, core-edge pairs), models pointed to dispersal facilitation in landscapes with abundant surface water and highway volume. Surface waters (wetlands, lakes, rivers) are not themselves sites for the container-breeding *Ae. albopictus*, but tend to be numerous where rainfall and relative humidity are high (e.g. southeastern USA; Fig. 1). Thus, connectivity may be facilitated where a higher density of container habitats is maintained (via climate) and stepping-stone dispersal is facilitated by reduced distances among local breeding sites. Highway connections were important at a broad spatial extent, but their significant correlation with genetic distance only between range-core and range-edge pairs suggests that dispersal to the current northern range limit is influenced by human-aided transport along highway corridors. Thus, efforts to prevent recolonization of eradicated sites towards the northern range limit and further northward spread should target containers that travel along interstate corridors that also contain cargo likely to harbour eggs and juvenile stages of mosquitoes (e.g. tires, nursery plants; Hawley *et al.* 1987; Farajollahi & Nelder 2009).

Models correlating genetic and landscape distance at a smaller spatial extent revealed negative relationships between agricultural land cover and forests. Conversion of land to agricultural land use since European settlement of the USA is also correlated with removal of isolated wetlands (McCauley & Jenkins 2005) and trees, and thus mosquito habitat in general. More importantly for *Ae. albopictus*, urban land cover and related density of artificial containers is reduced in areas where agricultural land use is dense and likely reduces habitat availability and access to stepping stones for dispersal and gene flow. At the range edge, forests hindered gene flow, even with extensive agricultural lands in the eastern Corn Belt and similarly mixed forest/agricultural land use throughout much of the rest of the range (see Fig. 1). We expected forests to facilitate gene flow because *Ae. albopictus* inhabits forest edges both as larvae in treeholes and as adults resting near areas with suitable oviposition sites. However, in a previous study, *Ae. albopictus* did not displace native *Ae. triseriatus* from treehole habitats in undisturbed wooded areas (Lounibos 2002). Thus, biotic resistance in forests may limit *Ae. albopictus* populations, effectively reducing gene flow across this habitat type. Moreover, forests may inhibit wind-mediated dispersal and provide a physical, habitat-complexity filter for *Ae. albopictus* migration.

The US introduction of *Ae. albopictus* into Houston, TX, in 1985 implicated the used tire trade for transporting propagules from SE Asia (Hawley *et al.* 1987; Craven *et al.* 1988), and subsequent spread across the USA was assumed to occur via similar routes (e.g. commercial or private vehicles) (Lounibos 2002). Our results support this hypothesis at the broadest spatial extent, and our spatially partitioned approach suggests that human-aided transport is currently biased to long-distance movement by highways between range-core and range-edge locations, but is likely dominated by natural movement at smaller distances. Thus, we hypothesize that the USA invasion had an initial human-aided spreading phase including jump-dispersal events followed by multinucleate diffusive spread via both local human-aided transport and natural dispersal. The spreading phase likely resulted from human-aided movement within the range and/or from additional introductions rather than natural dispersal; the rate of spread cannot be reconciled with the limited natural dispersal ability of this species (Hawley *et al.* 1987; Moore & Mitchell 1997). However, the genetic signature of that rapid spread is now only evident at the broadest spatial scale, and dispersal at smaller spatial scales is currently overwhelmed by a signature of natural dispersal, in part because sites throughout range core have become well established and abundant.

### *Methodological comparisons*

Consistent with previous work, our landscape genetics approach improved model fit compared to classic isolation by distance (McRae & Beier 2007; Jenkins *et al.* 2010). Using evidence ratios, we showed that landscape genetics models were orders of magnitude better than IBD. Previous work also showed a substantial improvement over IBD using resistance distances based on circuit theory (McRae *et al.* 2008). Our results showed that resistance distances were informative where dispersal was occurring across land-cover types that were continuous, such as farms and forest. Least-cost paths resulted in better model fit for models where dispersal occurred between discrete land-cover types (e.g. water availability, container habitat) or along highway corridors.

Contrary to expectations, cGD performed poorly relative to Dps in our study, potentially a result of effects of study scale relative to sampling density. Conditional genetic distance (cGD) was developed as a more realistic measure of gene flow, particularly when correlating gene flow with landscape features (Dyer *et al.* 2010; Garroway *et al.* 2011). As study extent increases and sampling density decreases, cGD may imperfectly assess genetic distance because of its reliance on topology among sites (Beerli 2004). However, cGD performs very well compared to traditional Fst-based distance measures (Dyer *et al.* 2010). Regardless, our results suggest that incorporating models with multiple genetic distance measures into model selection frameworks is useful, as distance measures may perform differently at different spatial extents. Thus, we advocate a multimodel selection approach to landscape genetics that includes alternative models and potentially multiple measures of genetic distance (Cushman & Landguth 2010).

### *Directions forward*

A major challenge ahead for landscape genetics and species invasions is understanding landscape effects on the distribution and spread of adaptive variation (Balckenhol *et al.* 2009). For our study system, the relationship between landscape features and variations in traits affecting overwintering success (i.e. diapause) could improve the understanding of northerly US range expansion beyond that predicted by species distribution models based on native climate (Medley 2010). The combination of human-aided dispersal and novel landscape permeability in invaded ranges may alter gene flow and shift adaptive potential for an exotic species relative to its native range. If background rates of gene flow are low, facilitated gene flow could provide the genetic material necessary for adaptation to occur,

particularly at range edges where populations are sometimes genetically and demographically depauperate, fragmented and subject to genetic drift (Holt 2003; Garant *et al.* 2007). Moreover, genetic admixture from multiple introductions could create hybrids that outperform founders (Geiger *et al.* 2011) or increase genetic variation sufficiently for adaptation to occur (Kolbe *et al.* 2004; Gillis *et al.* 2009). Indeed, many invasions have involved traits increasing invasive potential (Thomas 2001; Phillips *et al.* 2006), but whether these are consistently due to sampling effects from native source populations, genetic admixture or adaptation is unclear. Understanding the genetic consequences of landscape patterns on gene flow and adaptation, particularly for invasive species, is a promising avenue of continued research.

## Conclusions

Managing invasive species and disease risk are daunting tasks, but here we show how landscape genetics can be used to identify dispersal corridors and inform mitigation strategies. On the basis of our results, *Ae. albopictus* may be controlled by emptying accumulated water from artificial containers, and preventing the transport of eggs and immature stages in commercial shipments and in personal vehicles. The recommendation to remove container habitat is not new, but our results emphasize the importance of this practice to reduce local mosquito abundance and to eliminate sources of recolonization. Municipalities often spray larvicide or adulticide to manage mosquito populations, so focusing management efforts where source localities may contribute propagules to recolonization events – via natural dispersal or within commercial shipments – is important. At or near the northern range margin, timber harvest or conversion of forest to other land uses may facilitate *Ae. albopictus* dispersal and colonization events where the range may be expanding (Farajollahi & Nelder 2009).

Our results revealed a combined role of natural and human-aided dispersal throughout the range of *Ae. albopictus* only two decades after its initial introduction into the USA. Naturalized populations have become sufficiently dense that dispersal and recolonization are now naturally sustained, but long-distance dispersal, particularly between range-core and range-edge sites, is ongoing. A similar trend may be expected for introductions of other exotic species, particularly those that spread rapidly via human-aided transport and then establish dense, naturally connected sites. Our results affirm the importance of denying entry of exotic species as well as rapid responses to eradicate soon after introduction. In addition, multiple introductions can increase

genetic diversity and adaptive potential for some established invasive species (Kolbe *et al.* 2004; Gillis *et al.* 2009); potential ports of introduction should remain vigilant to continued importation of *Ae. albopictus* in used tires and other shipments with the potential to contain eggs and/or larvae from other continents where *Ae. albopictus* is now established. Finally, the spread of disease is often linked to human-aided transport, land-use change and climate-change (Crowl *et al.* 2008); recent advances in genetic and geographic techniques may improve the utility of landscape genetics as a viable assessment tool for mitigating disease risk, including disease vectors such as *Ae. albopictus*, at a global scale.

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K.A.M., D.G.J. and E.A.H. designed the study; K.A.M. performed the research and conducted the analyses; and all authors wrote the manuscript.

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### Data accessibility

Data and scripts have been archived with Dryad (doi:10.5061/dryad.4f0da).

### Supporting information

Additional supporting information may be found in the online version of this article.

**Table S1** Pairwise cGD (bottom left triangular matrix) and Dps (top right triangular matrix) among localities within the core and along the edge of the US range for *Ae. albopictus*. Comparisons within regions are shaded.

**Table S2** Landscape models, where the response was genetic distance (Dps or cGD) and the landscape distances were either least-cost path distance or resistance distance.