Modeling the Potential Dispersal of Asian Longhorned Beetle Using Circuit Theory

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The Asian longhorned beetle (ALB, *Anoplophora glabripennis*) is an invasive pest species currently infesting major port cities in North America and Europe. There is limited knowledge regarding the pathways of movement across heterogeneous landscapes at local scales. This study models dispersal pathways using circuit theory in Worcester, Massachusetts, which has the largest ongoing ALB infestation in North America. Circuit theory–based dispersal modeling provides a means of predicting the movement of random walkers across a landscape comprising differential resistance to movement. Calibration of landscape resistance to ALB movement used a combined expert opinion and empirical approach, with 820 ALB presence points for calibration and validation. Results indicate that ALB typically uses nonhabitat land-cover types to connect suitable habitat patches. Circuit modeling was a better predictor of spatial patterns of dispersal than least-cost dispersal modeling, especially by predicting narrow corridors that connect large habitat patches. ALB dispersal modeling is difficult due to limited data availability and ongoing ALB habitat modification. This article contributes to knowledge of ALB dispersal patterns at local and regional scales, using empirically driven methods to provide spatially explicit predictions of high dispersal probability and habitat suitability for ALB, using the best data sets available. **Key Words: Asian longhorned beetle, circuit theory, invasive species, urban forestry.**

亚洲天牛甲虫（ALB, *Anoplophora glabripennis*）是侵扰当今北美与欧洲主要港口城市的入侵害虫物种。但我们对其横跨地方层级异质地景的移动路径却所知甚少。本研究运用电路理论, 模式化在麻萨诸塞州伍斯特的传播途径, 该地遭受美国最大规模且持续的ALB侵扰。根据电路理论的传播模式化, 提供了工具来预测横跨包含不同移动阻力的地景之随机游走者的迁徙。抵抗ALB移动的地景校准, 运用专家意见与经验方法的结合, 并以八百二十个ALB出没点进行校准和验证。研究结果显示, ALB主要运用非栖地的土地覆盖类别来连结合适的栖息地块。电路模式化较最低成本传播模式化而言, 可较佳地预测传播空间模式, 特别是预测连结大型栖地的狭窄通道。由于有限的可及数据和持续的ALB栖地改变, ALB传播的模式化相当困难。 本文使用可及的最佳数据集, 运用经验驱动之方法提供ALB高传播可能性和栖地适宜性的明确空间预测, 对ALB在地方和区域尺度的传播模式之知识做出贡献。**关键词：亚洲天牛甲虫, 电路理论, 入侵物种, 城市森林。**

El escarabajo asiático cornilargo (ALB, *Anoplophora glabripennis*) es una especie de plaga invasora que actualmente está infestando las principales ciudades porteñas de América del Norte y Europa. Muy poco se sabe sobre la manera de su desplazamiento a través de paisajes heterogéneos, a escalas locales. En este estudio se modelan las rutas de dispersión por medio de la teoría del circuito cerrado en Worcester, Massachusetts, ciudad que actualmente registra la infestación de ALB más grande en América del Norte. El modelado de dispersión con base en la teoría del circuito suministra un medio de predicción del movimiento de caminantes aleatorios a través de un paisaje que presente resistencia diferencial al movimiento. La calibración de la resistencia del paisaje al movimiento del ALB usó una opinión experta combinada con un enfoque empírico, con 820 puntos de presencia para calibración y validación. Los resultados indican que el ALB típicamente usa tipos de cobertura de la tierra que no corresponden a su hábitat para conectar espacios que si son apropiados como hábitat. El modelado de circuito fue un mejor predictor de los patrones espaciales de dispersión que el modelado de costo mínimo, especialmente con la predicción de corredores estrechos que conectan grandes espacios de hábitat. El modelado de la dispersión del ALB se dificulta particularmente por la falta de disponibilidad de datos y el desarrollo de modificación del hábitat en la actualidad. Este artículo contribuye al conocimiento de los patrones de dispersión del ALB a escalas local y regional, usando métodos orientados empíricamente que generen predicciones de dispersión de alta probabilidad espacialmente explícitas y de hábitats idóneos para el ALB, usando los mejores conjuntos de datos disponibles. **Palabras clave: arbolados urbanos, escarabajo asiático cornilargo, especies invasivas, teoría del circuito cerrado.**

Invasive species represent a significant threat to ecological and economic systems across geographic scales (Lowe et al. 2000; Pimentel, Zuniga, and Morrison 2005). The Asian longhorned beetle (ALB, *Anoplophora glabripennis*) is a polyphagous, wood-boring beetle native to China and Korea and has been listed as one of the 100 worst alien invasive species (Lowe et al. 2000). ALB has spread via infested packing materials to major port cities in North America and Europe (Haack et al. 2010), where the species has no known predators and infests a wide range of tree species (Haack et al. 2010; Meng, Hoover, and Keena 2015). Left unchecked, ALB reduces tree cover and associated ecosystem services in cities (Nowak et al. 2001; Raupp, Cumming, and Raupp 2006). Although ALB infestations have primarily been in urban areas (Hu et al. 2009; Haack et al. 2010), the beetle also poses a threat to wildland forest ecosystems (Sawyer et al. 2011; Dodds and Orwig 2011). A wide range of

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forests across the United States are at risk (Kappel et al. 2017), with regional dispersal caused by unintentional movement of infested lumber and firewood (U.S. Department of Agriculture Animal and Plant Health Inspection Service [USDA-APHIS] 2014).

Nonanthropogenic ALB dispersal in novel environments is limited by the insect's slow rate of movement and tendency to continually infest the same tree for several years (Meng, Hoover, and Keena 2015). ALB is capable of dispersing by walking or flying short distances of typically under one kilometer over an individual's life cycle (Hu et al. 2009; Meng, Hoover, and Keena 2015; Trotter and Hull-Sanders 2015). There is limited understanding of specific obstacles to and facilitators of ALB movement during dispersal at the local scale (Sawyer et al. 2011). For infestations adjacent to the wildland–urban interface, local-scale dispersal pathways across heterogeneous landscapes are a significant risk, particularly due to the high cost of eradication (Dodds and Orwig 2011). Therefore, to aid ongoing eradication efforts, it is critical to understand ALB dispersal behavior through novel environments. This article seeks to contribute to the understanding of the dispersal characteristics of ALB in urban and wildland environments.

Asian Longhorned Beetle

Initial ALB infestations in North America were reported in New York City in 1996 (Haack et al. 1997), with subsequent infestations in Chicago in 1998 (Poland 1998); Jersey City, New Jersey, in 2002 and 2004 (Haack 2006); Toronto in 2003 (Canada Natural Resources 2016); Worcester, Massachusetts, in 2008 (Haack et al. 2010; Dodds and Orwig 2011); Boston in 2010 (USDA-APHIS 2014); and Clermont County, Ohio, in 2011 (USDA-APHIS 2013). European infestations have been located in Austria, France, the United Kingdom (Straw et al. 2016), Germany, and Italy, between 2001 and 2012 (Haack et al. 2010; Faccoli et al. 2015; Meng, Hoover, and Keena 2015). The ALB infestation in Worcester represents the largest infestation in North America to date and is an ongoing management challenge (Santos and Cole 2012; Worcester Tree Initiative 2015; Danko et al. 2016).

As larvae, ALB consume the cambium and then heartwood of infested trees, before pupating and tunneling out of the tree. The beetle matures between one and two years after oviposition (Haack et al. 2006; Hu et al. 2009; Meng, Hoover, and Keena 2015). Repeated infestation of a host over multiple generations ultimately weakens and kills the tree (Nowak et al. 2001). Infested trees represent a direct threat to humans and property, particularly during severe weather events (Hostetler et al. 2013). Loss of trees reduces ecosystem services, including air and water filtration, canopy shading, and stormwater runoff control (Akbari, Pomerantz, and Taha 2001; Xiao and McPherson 2002; McPherson and Simpson 2003; Pandit and Laband 2010; Nowak et al. 2013; Nowak et al. 2014). A widespread wildland infestation could have a large economic impact due to decreased resources for lumber and tourism industries (Liebhold et al. 1995; Nowak et al. 2001; Stadler et al. 2005; Raupp, Cumming, and Raupp 2006; Hejda, Pyšek, and Jarošík 2009).

ALB tend to reinfest their natal host tree and show slow natural dispersal (Zhou, Zhang, and Lu 1984; Meng, Hoover, and Keena 2015). When the host quality declines, beetles disperse to new hosts by flying or walking (Meng, Hoover, and Keena 2015), generally moving between 100 and 3,000 m from their natal tree (Junbao et al. 1998; Smith et al. 2001; Smith et al. 2004; Bancroft and Smith 2005; Haack et al. 2010). The dispersal phase lasts up to about 200 days (Keena 2006), and the majority of beetles disperse under 1,000 m (Smith et al. 2001; Smith et al. 2004). It is possible that ALB seek new hosts by detecting and moving toward potential host trees using plant or conspecific odors (Meng, Hoover, and Keena 2015), demonstrating modest host-seeking behavior over short distances. Based on the beetle's slow natural dispersal rate, adjacent host trees are most at risk for new infestation (Favaro et al. 2015). Human movement of infested wood is an important driver of regional-scale dispersal, however (Haack et al. 2010).

To avert the spread of ALB, eradication efforts have relied primarily on host tree removal and destruction within specified regulation zones (Sawyer 2007; USDA-APHIS 2008). APHIS relies on intensive field surveying for ALB detection (Nehme et al. 2014), with surveys conducted within a 2,400-m buffer of previously infested and removed trees and resurveying for two years after removal of high-risk or infested trees (Haack et al. 2010). Such surveys have necessitated the inspection and reinspection of millions of trees within the Worcester regulation zone (192 km^2). Spatially explicit dispersal maps would greatly increase surveying efficiency.

Modeling Invasive Species

Predicting the geographic dispersal of invasive species has been an important yet difficult goal for management efforts, with contributions from the fields of landscape ecology, entomology, population biology, and GIScience (Liebhold, Halverson, and Elmes 1992; Peterson 2001; Call and Nilsen 2003; Huebner 2003; Austin 2007; Brown, Spector, and Wu 2008; Elith and Leathwick 2009; Morin, Liebhold, and Gottschalk 2009). Several distinct methods have been used to determine and map locations vulnerable to new invasion, in general focusing on either characterization of preferred habitat (Austin 2007; Elith and Leathwick 2009) or modeling the mechanism of movement across the landscape (Liebhold, Halverson, and Elmes 1992; McRae et al. 2008). Therefore, research tends to focus on either habitat suitability or the rates and pathways of diffusion.

Species distribution modeling (SDM) uses statistical characterization of presence points to create a continuous prediction of habitat quality (Peterson 2001, 2003; Brown, Spector, and Wu 2008; Elith and Leathwick 2009) and is particularly useful in determining long-term invasion potential under the assumption of equilibrium (Roura-Pascual et al. 2009; Václavík and Meentemeyer 2012). Spatial diffusion modeling focuses on rates of population growth and geographic expansion of species range over time (Skellam 1951; Andow et al. 1990; Liebhold et al. 1995), predicting the dynamic spread of species. Such modeling is typically made at regional and larger scales, and many use an isotropic or generalized model of landscape resistance to movement (Liebhold, Halverson, and Elmes 1992; Tobin, Liebhold, and Roberts 2007; Liebhold and Tobin 2008). At local scales with high landscape heterogeneity, this approach might present an incomplete model of dispersal risk (McRae 2006; McRae et al. 2008; Etherington et al. 2014).

Trotter and Hull-Sanders (2015) used graph theory to determine the topological connections between infested trees, which can then be used to calculate rates of movement across a landscape. Order of infestation is valuable for modeling pathways of dispersal because it provides the sources and destinations of the beetles, but graph theory does not consider landscape composition of the space between ALB presence points, which is treated as an isotropic plane of equal resistance. Least-cost approaches to animal movement incorporate heterogeneous landscape composition, calculating the relative difficulty of reaching any given location based on calibrated resistance by quantifying the sum of resistances along the most efficient path (Singleton and Gaines 2002; Chardon, Adriaensen, and Matthysen 2003; Etherington et al. 2014; Shatz et al. 2016). Even low-quality habitat might serve as a corridor for animal movement at localized spatial extents and individual insect life spans, so it is important to consider habitat suitability and resistance to dispersal separately. Resistance, also called friction, reflects the relative ease of dispersal across a pixel. Previous research has modeled ALB dispersal using least-cost path modeling (Shatz et al. 2016), but because ALB are random walkers, it is not ideal to model them as agents that select the optimal path between two points (McRae et al. 2008; Beier et al. 2011).

The research presented here uses dispersal modeling based on an analogy to electrical circuit modeling (McRae et al. 2008; Shah and McRae 2008). The circuit theory approach models species movement as electrical conductance, representing a series of random walks by the dispersing animal over a resistance layer constructed from environmental data (McRae et al. 2008; Shah and McRae 2008). This approach is different from least-cost analysis in that dispersal is modeled over all possible paths (McRae 2006). Least-cost modeling assumes that the disperser has prior knowledge of a final dispersal location and selects only the optimal path to reach that location, which does not accurately model beetle movement.

Both circuit and least-cost approaches rely on a resistance layer to define relative difficulty of movement across each pixel (Singleton and Gaines 2002; McRae 2006; Zeller, McGarigal, and Whiteley 2012). Calibration of resistance rasters typically relies on a combination of expert opinion and empirical approaches (Zeller, McGarigal, and Whiteley 2012). Calibrated models can provide dispersal pathways that highlight locations and paths of high “traffic,” also called pinch points, that can improve surveying, eradication, and overall management efforts.

This research investigates the impact of heterogeneous landscapes on the ongoing ALB infestation in and adjacent to Worcester, Massachusetts. Predictions of dispersal probability are combined with a metric of habitat quality to create a combined dispersal- and habitat-based risk assessment. This contributes to (1) general knowledge of ALB dispersal by identifying optimal landscape variable configurations and calibrations and (2) the more immediate needs of ALB eradication in central Massachusetts by identifying ALB movement corridors. High dispersal probabilities adjacent to the regulation zone boundaries constitute a significant threat to the success of the eradication program and therefore constitute essential information for USDA-APHIS.

The research goals of this article are as follows:

1. Use existing information on ALB presence and order of infestation, combined with a model of landscape resistance to ALB movement, to determine dispersal likelihood for ALB using a circuit theory dispersal model.
2. Compare circuit theory dispersal predictions to a more conventional least cost–based dispersal model.
3. Combine predictions of potential ALB dispersal with predictions of high-quality ALB habitat to produce an overall assessment of potential infestation.

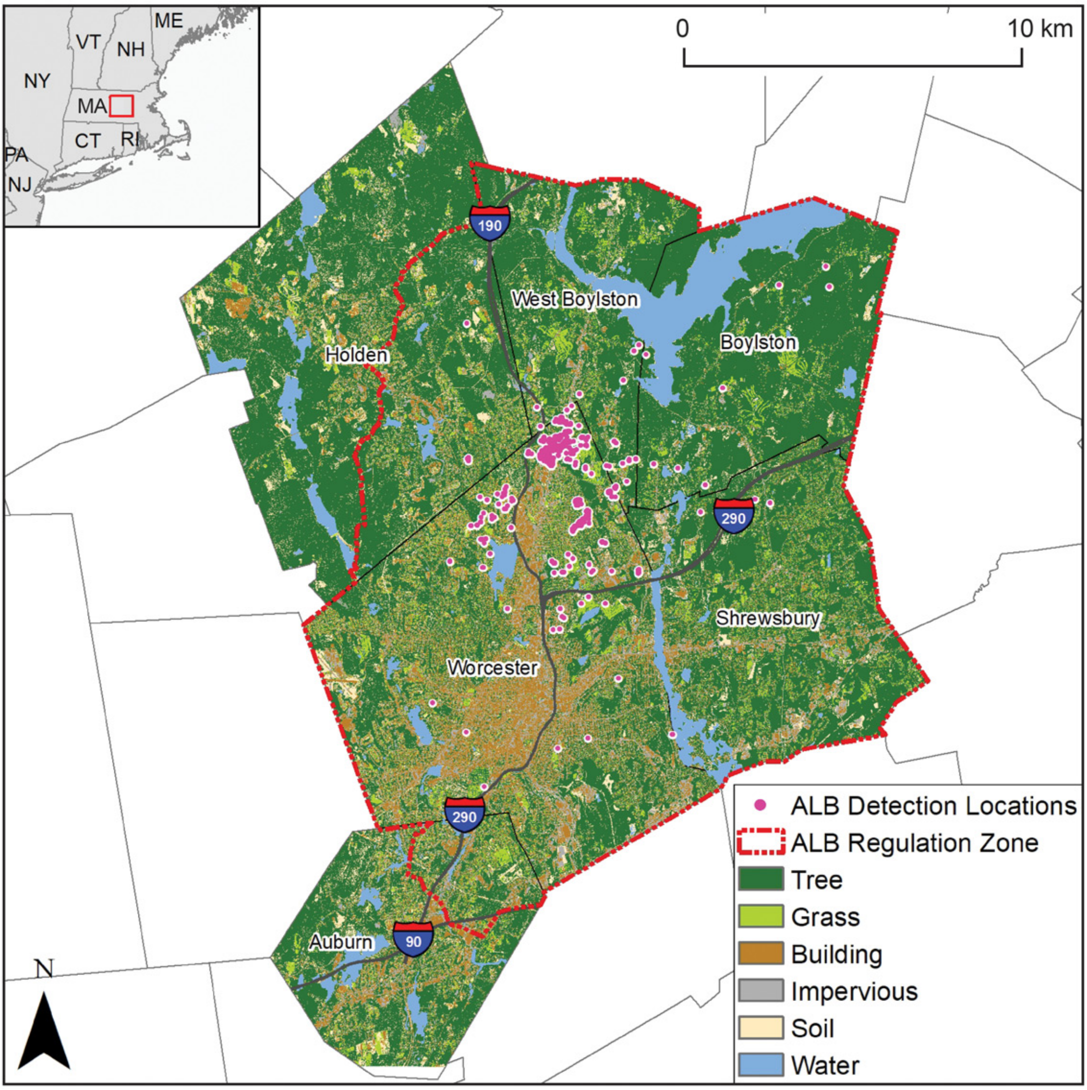

Figure 1 *Study area, showing ALB–infested host trees. The red line indicates the extent of the U.S. Department of Agriculture Animal Plant Health Inspection Service ALB regulation zone, which is currently containing the infestation in this area. This map shows land-cover mapped at 0.5-m spatial resolution, using satellite imagery acquired in May 2015. ALB = Asian longhorned beetle. (Color figure available online.)*

Study Area

The study area in central Massachusetts centers on Worcester and includes parts of five adjacent towns included in the USDA regulation zone (Figure 1). Worcester contains a large number of ALB host trees, partially due to urban forestry efforts in the twentieth century (Herwitz 2001; Freilicher et al. 2008). A large number of *Acer* species, a preferred host for ALB (USDA-APHIS 2008), were planted adjacent to streets (Freilicher et al. 2008), creating an edge habitat ideal for ALB (Williams, Lee, and Kim 2004).

The ALB infestation in central Massachusetts is the only known instance in which ALB have dispersed from urban areas into closed canopy forests, which is a threat to the broader northern hardwood forests in New Hampshire, Vermont, and Canada (Dodds and Orwig 2011). It is likely that ALB was transported to Worcester via wooden shipping pallets, with the earliest infested trees found near an industrial wood packing material holding site in 2008 (Trotter and Hull-Sanders 2015) and speculated infestation onset up to a decade prior to that date (Hammel 2008; Danko et al. 2016). ALB spread to the adjacent residential neighborhoods of Burncoat and Greendale, traversing approximately 0.6 km of industrial land use, forest edge, and open space. ALB are typically observed in edge habitats (Williams, Lee, and Kim 2004; Sawyer et al. 2011) and might exploit fragmented or perforated landscapes (Sawyer et al. 2011) such as the wildland–urban interface land covers constituting the study area. ALB presence was detected within the regulation zone as late as 2016 and 2017, even after the removal of about 35,000 host trees to curb the infestation (Santos and Cole 2012), highlighting the need for enhanced knowledge of ALB dispersal behavior.

Data and Methods

Data

ALB presence was inferred from the location of infested host trees. These data ($n = 820$) also indicate the level of infestation, which was previously used to infer order of infestation in the study area (Trotter and Hull-Sanders 2015). Infestation order determined source and destination trees for dispersal model calibration and validation. Presence locations were subdivided into five subsets:

- Subset 1, the original infested tree, infested since at least 1999 (Sawyer et al. 2011).
- Subset 2, the next 13 infested trees.
- Subset 3, the next 52 trees.
- Subset 4, the next 708 trees.
- Subset 5, the most recently reported 46 infested trees in 2016.

Four dispersal intervals can be inferred from these subsets, with one interval between each adjacent pair of subsets. The decline in the number of ALB infestation presence points between subsets 4 and 5 can be attributed to the USDA-APHIS eradication effort. It was not possible to attribute a specific year to any infestations (Trotter and Hull-Sanders 2015), with the exception of subset 5, which was attributed to 2016 by USDA-APHIS.

The heterogeneous study area was modeled by a composite friction surface representing barriers to and facilitators of dispersal (Wade, Mckelvey, and Schwartz 2015). Friction was modeled using land cover and distance to the nearest tree, both measured at 0.5-m spatial resolution. Land cover represents physical impediments to beetle movement at the local scale. Six land-cover categories were used: bare ground, grass or shrub, tree, impervious surface, building, and water. This land-cover classification was created using 0.5-m WorldView-2 imagery with RandomForests classification (Elmes et al. 2017). The distance to tree raster incorporates the beetle's host-seeking drive, which makes a beetle less likely to stray farther away from possible host trees (Meng, Hoover, and Keena 2015). Whereas the circuit model reflects unbiased random walks, the inclusion of distance to tree slightly modifies the aggregated dispersal characteristic such that it effectively reflects a biased random walk (sensu Codling, Plank, and Benhamou 2008).

ALB Dispersal Modeling

In total, seventy-two circuit theory dispersal models were compared to an equal number of least cost–based dispersal models using the same underlying beetle presence and environmental data sets. The more widely used least-cost approach was used as a basis for comparison.

To use the principles of electrical current theory for landscape dispersal modeling, the following analogies are taken from McRae et al. (2008). Resistance, measured in ohms, is the opposition to current provided by a given resistor. In landscape applications, this feature measures the difficulty of passage over a given pixel, also called friction. Current, measured in amperes, quantifies the flow of charge flowing through a series of resistors, in this case a path of pixels (McRae et al. 2008). Current is measured and combined over all possible paths, therefore predicting net movement probabilities for random walkers over the landscape (Doyle and Snell 2000; McRae et al. 2008).

Resistance Raster Creation Resistance surface modeling was a focal point of this analysis, as appropriate characterization of resistance to ALB movement dictates where and how species will disperse (Zeller, McGarigal, and Whiteley 2012; McRae, Shah, and Mohapatra 2013; Etherington et al. 2014). Circuit-based dispersal was modeled for each candidate resistance parameter in turn, using a 70 percent to 30 percent random split of presence points for calibration and validation. The presence data set was subdivided into source and destination points for each of the four previously defined time intervals. Optimal calibration was inferred from the ratio of mean current values (i.e., presence probability) at validation locations versus the same value at pseudoabsence points. Pseudoabsence locations, representing plausible presence locations where no ALB have been found, were randomly generated within intermediate distances (250–3,000 m) from known presence locations, following VanDerWal et al. (2009). The validation:pseudoabsence ratio was also calculated for the cost-distance method, providing a direct comparison metric between the two methods because the division negates any potential difference in data value range. A high validation: pseudoabsence ratio indicates high dispersal probability at known validation points and low predicted probability at absence locations, meaning a higher quality prediction.

The resistance raster was constructed by combining land use and distance to tree rasters in several configurations, running the dispersal model using

Table 1 *Resistance raster calibration and validation*

Order	Ramp	Distance weight	Overall mean of validation to pseudoabsence ratio for circuit dispersal	Overall mean of validation to pseudoabsence ratio for least-cost dispersal
1	NoRamp	25	631.0	4.1
	NoRamp	50	531.0	4.1
	NoRamp	75	415.4	4.0
	e	25	455.7	4.5
	e	50	510.1	4.0
	e	75	672.0	3.8
	10	25	439.8	3.8
	10	50	584.6	3.4
	10	75	536.0	3.1
2	NoRamp	25	592.7	4.1
	NoRamp	50	553.6	4.1
	NoRamp	75	553.6	4.1
	e	25	428.7	4.5
	e	50	512.0	4.0
	e	75	628.0	3.6
	10	25	409.6	2.8
	10	50	392.8	3.1
	10	75	452.6	3.4

Notes: The order column indicates the order of land-cover classes, and the ramp column indicates the exponential increase in resistance, starting from the first land-cover class.

the appropriate calibration points, and using the validation:pseudoabsence ratio to define the optimal combination (Beier, Majka, and Newell 2009; Zeller, McGarigal, and Whiteley 2012; Etherington et al. 2014). The six land-cover categories were ranked in two orders of increasing resistance to movement, based on expert opinion and literature. The first order (Order 1) was ranked as follows, with increasing resistance: impervious, bare ground, grass, tree, building, and water. The second order (Order 2) grouped land-cover classes as (1) impervious, bare ground, and grass and (2) tree and building. In both cases, the water category was treated as an absolute barrier to dispersal. These two orders represent candidate ranks of land-cover resistance, but there was no clear reason to assume a linear increase in resistance. Therefore, in addition to the simple linear increase in resistance, two power functions (*e* and 10) were used to exponentially increase the resistance of each subsequent land-cover class (Beier, Majka, and Newell 2009; Etherington et al. 2014). This produced three land-cover resistance "ramps" for each order, yielding six candidate resistance rasters. A final consideration was the influence of distance to tree, representing host-seeking behavior. Inclusion of this raster relied on a weighted linear combination with the six previously described rasters. Because no a priori knowledge of appropriate weights was available, and due to the intensive computational demands of circuit theory analysis, three weightings were used for distance to trees: 0.25, 0.5, and 0.75, with the corresponding fraction of the weight given to the land-cover raster. This produced eighteen candidate resistance rasters for use in model calibration. Due to the five time intervals, a grand total of seventy-two calibration models were tested.

ALB Dispersal to Novel Environments ALB dispersal was modeled using the optimal resistance raster, starting from the most recently infested trees and progressing outward. This was accomplished by setting the "ground" required by an electrical circuit to the ALB regulation zone boundary (red dashed line in Figure 1). For comparison, least-cost dispersal analysis was also conducted using the same ALB presence and resistance inputs. Least-cost dispersal probability was estimated as the inverse of least-cost distance. Quantitative comparison of least-cost and circuit theory approaches was based on the validation:pseudoabsence ratio.

Combined Habitat and Dispersal Risk Assessment A combined ALB risk map was created by combining high-quality habitat with high-probability dispersal locations. Habitat quality was modeled using a maximum entropy (Maxent) model, created previously by Shatz et al. (2016). The habitat map was thresholded at a value of 0.25, which, according to Shatz et al. (2016) indicates a medium to extreme risk for ALB inhabitation, indicating preferable ALB habitat relative to the study area. This yielded a binary map of high-quality habitat, which was overlaid with the dispersal map to produce risk. Overall risk incorporates the disparate but complementary elements of dispersal and the successful infestation and reproduction of the beetle.

Results

Resistance Raster Calibration

Resistance raster calibration results in Table 1 show the ratio of the mean dispersal probability for

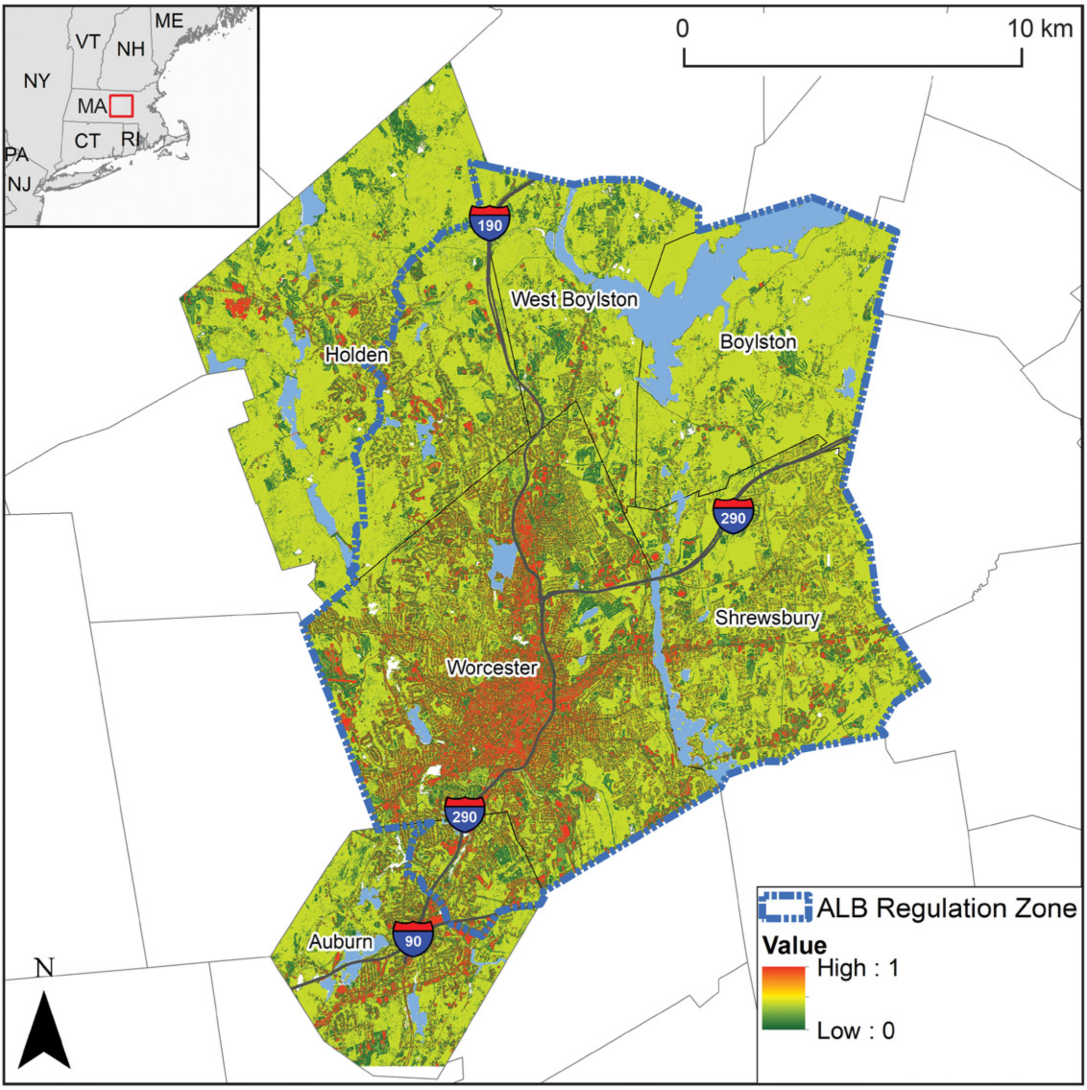

Figure 2 *Resistance to ALB movement across the study area landscape. This map reflects the final calibration of landscape resistance that best described ALB validation data. ALB = Asian longhorned beetle.*

validation and pseudoabsence points. The optimal calibration used land-cover Order 1, with land-cover resistance increasing as a natural exponent of land-cover category rank (*e*) and a weighting of 0.75 for the land-cover raster, with the remaining 0.25 for distance to trees. The map in Figure 2 shows the final calibration of resistance to ALB movement.

ALB Dispersal to Novel Environments

Circuit-based dispersal from the most recent ALB presence locations (2016) to the perimeter of regulation zone is shown in Figure 3, illustrating the tendency of circuit theory to "find" all possible paths of dispersal, indicated by the brighter yellow pixels. This pattern is even more apparent when viewed in finer spatial detail (Figure 4).

A direct comparison of the circuit theory and least-cost dispersal approaches (Figure 5) shows the fundamentally different nature of the spatial predictions made by these two methods: least-cost dispersal (Figure 5B) produces a smooth decrease in probability as a function of distance from low-friction surfaces, whereas circuit theory dispersal produces a more nuanced prediction, combining distance decay with prediction of narrow, high-probability pathways through the friction landscape. This pair of maps shows several of the most recently detected ALB locations in 2017, relative to presence locations from the previous year, 2016. The least-cost approach does not model landscape connectivity via pinch points and does not show high prediction probabilities for withheld validation points relative to pseudoabsence points, even

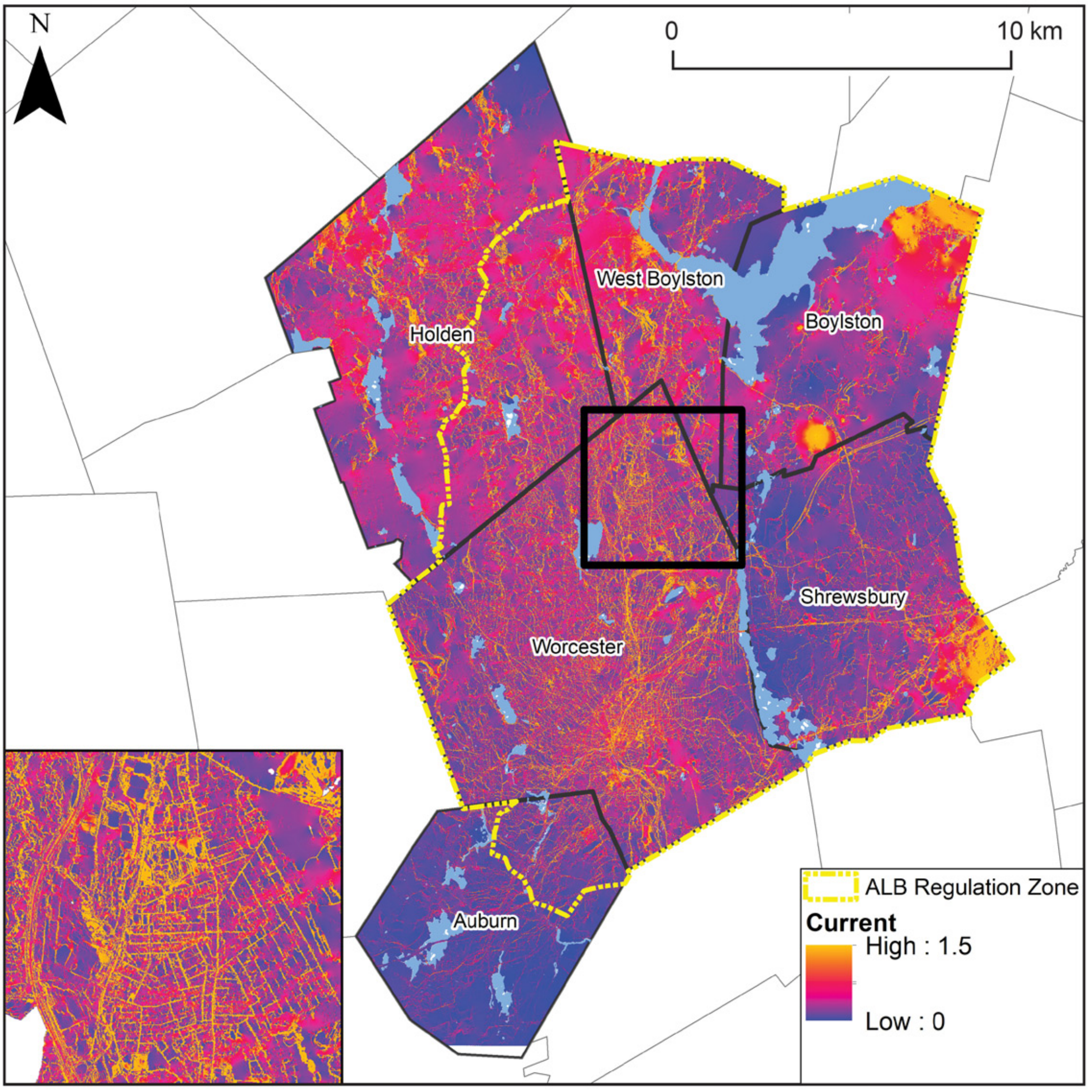

Figure 3 *Map of potential ALB dispersal using circuit theory. The inset map shows the Burncoat and Greendale neighborhoods of Worcester, the first residential neighborhoods affected by the ALB infestation. ALB = Asian longhorned beetle.*

though it includes the same environmental friction model as the circuit theory approach. The narrow branches of high current predicted by the circuit model qualitatively appear to connect known ALB presence locations from different years and, more important, the circuit theory map illustrates a much higher validation:pseudoabsence ratio than the least-cost approach (Table 1). In fact, all landscape calibrations produced substantially higher validation:pseudoabsence ratios for circuit theory models than least-cost models, with all circuit-based values >400 and all least-cost-based values <1. Although these values appear incommensurate based on the difference in magnitude, they are in fact directly comparable.

Combined Habitat and Dispersal Risk Assessment

Although many of the highest risk locations shown in Figure 6A lie adjacent to recently eradicated infestations, the outlying areas show important information regarding potential ALB dispersal (Figure 6). Locations to the north and northwest of the regulation zone contain extensive high-quality habitat but are not as permeated by roads and therefore show low ALB dispersal probabilities. Similarly, the eastern portion of the regulation zone, in the town of Shrewsbury, shows intermediate values of dispersal probability caused due to the screening effect of the Quinsigamond Reservoir, with rapidly increasing dispersal probabilities toward the southeastern-most point of the regulation zone. Because the habitat quality is intermediate and spatially patchy in this area, however, the overall risk of ALB establishment is low. The northeastern section of the regulation area also shows high dispersal probability. Here, the habitat is also somewhat spatially dispersed but, due to high dispersal probabilities included in the patches of high-quality habitat, this area is at high risk for potential ALB infestation. These high-risk areas are connected to previously infested landscapes by a relatively narrow corridor directly south of the Wachusett Reservoir. The lowest dispersal probabilities lie in the southern extreme of the regulation zone, in the town of Auburn. Although ALB habitat is extensive in this location, the low probability of dispersal means that this area is of lower concern to ALB spread.

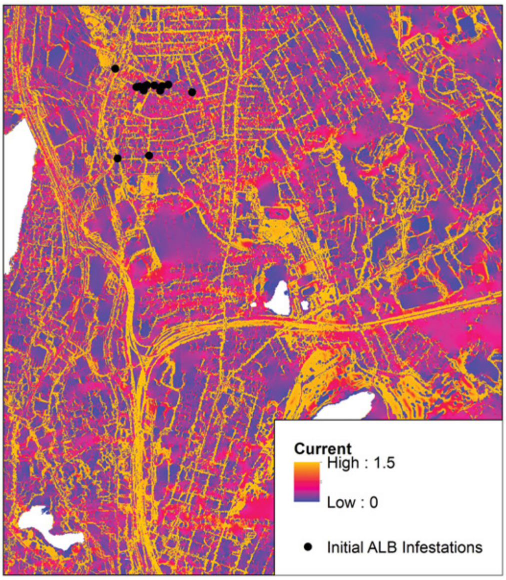

Figure 4 *Current map of ALB dispersal, showing the approximate location of the initial infestation of ALB in Worcester. The map indicates dispersal probability (current), illustrating the ability of circuit theory dispersal to "find" all possible routes. ALB = Asian longhorned beetle. (Color figure available online.)*

Discussion and Conclusions

Circuit theory is well suited for mapping landscape connectivity due to its ability to locate narrow pinch points, which is essential for invasive pest management because they might connect larger habitat patches. Results indicate that pinch points connect the core infestation area with novel dispersal environments toward the boundaries of the regulation zone (Figures 3 and 6), yielding higher quality predictions than least-cost dispersal when considering the validation:pseudoabsence ratio. Circuit theory consistently predicted higher dispersal probability at withheld validation points than at the pseudoabsence points, when compared to the least-cost approach, the predictions of which were far more spatially uniform and had far lower validation ratios. The combined risk map showed that several locations with high dispersal probability had nonsuitable habitat conditions, whereas other locations with intermediate dispersal

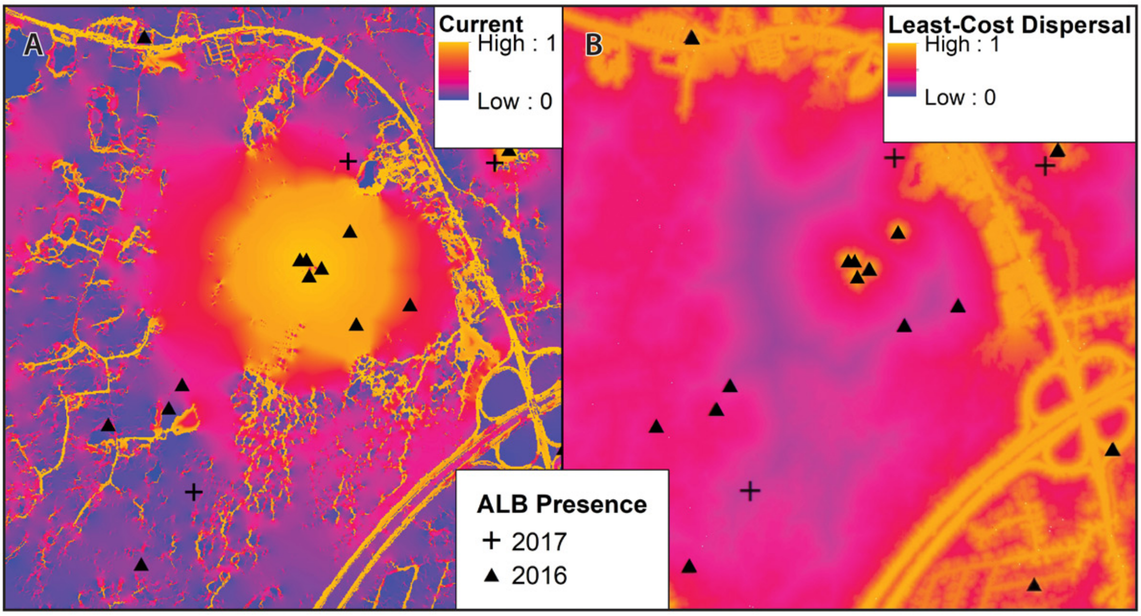

Figure 5 *Map of potential ALB dispersal based on (A) circuit theory dispersal and (B) least-cost dispersal. The maps also show observed ALB locations in 2016 and 2017. ALB = Asian longhorned beetle. (Color figure available online.)*

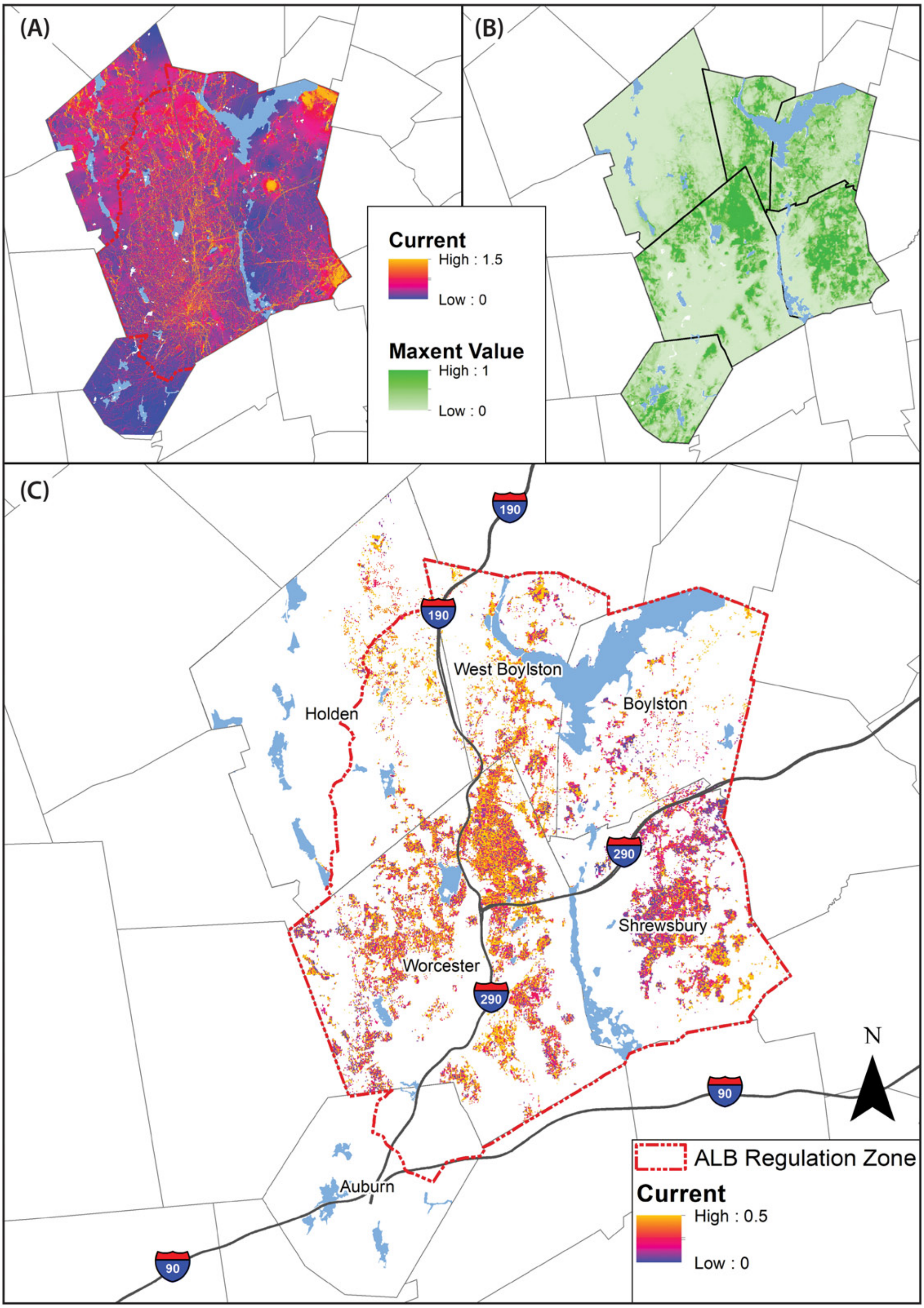

Figure 6 *Map showing the intersection of (A) predicted future ALB dispersal (measured by current; i.e., probability of dispersal per pixel) and (B) high-quality habitat (via Maxent value). (C) The combined risk map has been thresholded based on the Maxent model, such that it shows only medium, high, and extreme quality of ALB habitat (>0.25); white areas are either below the habitat quality threshold or are outside the study area. ALB = Asian longhorned beetle.*

probability showed high habitat suitability, highlighting the importance of considering both ALB dispersal and habitat quality together.

Resistance Raster Creation

Calibrating the resistance surface is often the most challenging step of dispersal modeling, because landscape effects on individual movement patterns are rarely known. The data-driven method used here combined ALB presence data with knowledge of the study area and ALB movement to limit the number of potential configurations of environmental variables, while still allowing a wide range of calibration settings (seventy-two candidate models). Limiting the number of candidates was necessitated by computational limits, with production of circuit-based maps requiring between two and twelve hours on a desktop workstation (3.6 GHz, quad core processor, 16 GB memory).

The impervious surface, bare soil, and grassland covers contain fewer obstacles to flight-based dispersal than tree, building, and water classes (Sawyer et al. 2011), and impervious surface (e.g., roads) also contributes information of anthropogenic movement of infested wood, allowing for longer distance dispersal pathways. Such dispersal is likely to have occurred within the Worcester ALB regulation zone (Haack et al. 2010; Meng, Hoover, and Keena 2015; Trotter and Hull-Sanders 2015), with the most recent ALB observations geographically dispersed from the initial infestation area but located within close proximity to roads. Another important contribution of the impervious, bare soil, and grassland covers is that they represent locations directly adjacent to the forest edge habitats favored by ALB (Williams, Lee, and Kim 2004; Dodds and Orwig 2011; Sawyer et al. 2011). Results indicate that it is beneficial to subdivide these low-profile categories individually, rather than rely on broader groupings, because Order 1 provided better results than the more aggregated Order 2. Additionally, the contributions of the land-cover categories were found to increase exponentially with rank order, implying that impervious covers are vastly lower resistors to movement than forest. Future work will further investigate these nuances of resistance map construction.

ALB Dispersal and Risk Modeling

Previous research on animal movement has used least-cost distance to quantify the cumulative effort of movement across heterogeneous landscapes (Etherington et al. 2014; Shatz et al. 2016). This method, however, calculates the accumulated cost of movement only over the path of least resistance, which does not accurately reflect that of beetles, whose dispersal is more accurately reflected by the random walk of circuit theory, with highly localized host-seeking movement incorporated in the resistance layer. The aggregate dispersal pattern produced by this analysis is therefore best described as biased random walk (sensu Codling, Plank, and Benhamou 2008).

The disparity between the two approaches is indicated clearly by Figure 5. The least-cost method produces a pattern similar to a dispersal kernel across an isotropic landscape. Circuit-based dispersal modeling explores all possible paths, which is similar to the aggregated movements of many independent, nonintelligent beetles. Although no individual disperser knows the best route between two locations, the aggregate of many random walks, attenuated by differentiated resistance, yields a map of landscape connectivity. Pinch points connect initial infestation location to the outlying regions, particularly along the southern edge of the Wachusett Reservoir, and along Interstates I-190 and I-290 (Figures 3 and 6). Compared to the least-cost model shown in Figure 5, the circuit model produced a more nuanced and differentiated spatial pattern, with narrow corridors infiltrating potential new habitat, still focusing most prediction on locations directly adjacent to previously infested trees—in keeping with known ALB movement characteristics. Although the narrow pathways of high dispersal likelihood appear to connect presence locations from different years, this pattern should be interpreted as a probabilistic rather than deterministic indication of infestation. As compared to least-cost methods, which produced diffuse, proximity-dominated predictions, circuit theory predictions were spatially more coherent and focused on potential linking pathways, many of which were unintuitive but nevertheless corroborated by the validation data. This could help to more efficiently deploy beetle detection survey teams and resources; for example, by using these narrow pathways as baselines for spatial buffers within which to conduct intensive surveying. Although some of these insights are qualitative in nature, they nevertheless provide valuable information to land managers in investigating the spread of ALB in situ. Quantitative validation, presented in Table 1, reinforces the value of this conclusion.

Results indicate that land cover is an important constraint on beetle movement and that more finely differentiated categories provided more accurate predictions. The best calibrated resistance model used land-cover Order 1, with impervious surfaces as lowest resistance, followed by bare ground, grass, tree, building, and water. In contrast, the less successful Order 2 consolidated the land-cover categories into two large classes. Distance to trees was found to be less important than land-cover type, as the optimized resistance raster used a weighting of 0.25 for this raster compared to 0.75 for the land-cover raster. This indicates that although ALB's host-seeking behavior might have some importance, land-cover resistance dominates the city-scale patterns.

Combined dispersal and habitat models yield overall risk of ALB infestation. The locations at highest risk are along the southern extent of the Wachusett Reservoir and along the route of Interstates I-190 and I-290 north of Worcester (Figure 6). Removing nonsuitable habitat reduced ALB risk areas considerably, allowing for more targeted and focused ALB surveying and eradication. The combination of a circuit theory dispersal model with a static habitat suitability model provides information on both the dynamic movement of individual beetles and the locations most amenable to new infestation and reproduction. Compared to least-cost movement models, the circuit-based approach has a closer conceptual linkage to individual ALB movement and also provides more accurate spatial predictions of their presence. Both approaches rely on accurate landscape resistance calibration, however, and based on the computationally intensive nature of circuit modeling compared to least-cost modeling, this represents a potential drawback of the approach. Future work could further strengthen these models by incorporating additional presence data from subsequent years and could explore the possibility of adding additional environmental layers to the resistance surface calibration approach laid out here. It might also be beneficial to develop parallel processing approaches that would facilitate the calibration process. It would be particularly interesting to apply these methods to different ALB infestation locations, such as the more recent outbreak in Bethel, Ohio, which has a quite different physical and cultural landscape. Understanding gained from these analyses could greatly aid land managers at local and regional scales, contributing to the global problem of invasive species. ■

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