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Quantifying Dispersal of the Asian longhorned beetle (*Anoplophora glabripennis*, Coleoptera) with incomplete data and behavioral knowledge

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Abstract Eradication programs for invasive species can benefit from tools that delineate infestations and identify patterns of spread to guide eradication priorities and activities. However, identifying these patterns in cryptic organisms such the Asian longhorned beetle can be complicated by the sometimes conflicting needs of rapid eradication and research. Here, we describe the use of a simple approach based on tools and concepts used in graph theory to infer beetle movement, using infested tree records collected by the Asian Longhorned Beetle Eradication Program in Worcester, MA, the largest infestation yet found in the U.S. Analyses included two sets of assumptions about beetle dispersal (representing a gap in knowledge of beetle biology), and two data sets of varying completeness, which were combined to develop and compare four scenarios of beetle dispersal in Worcester, MA. Together, these four scenarios suggest that the shape of the beetle dispersal-distance probability curve or dispersal kernel is more sensitive to assumptions about the predilection of beetles to disperse than to the size and completeness of the infested tree database, though both impacted inferred patterns of dispersal. The four scenarios are used to produce empirical estimates of dispersal risk around the current infestation, which can inform eradication efforts while recognizing the limits of data availability in a rapidly evolving eradication program. These estimates of dispersal also highlight the importance of continuing to integrate data collection into eradication programs, and the need to expand our understanding of beetle behavior and biology, as the data shown suggest that differences in dispersal behavior could dictate different eradication strategies.

Keywords Invasion dynamics · Population spread · Dispersal kernel · Host adjacency

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Introduction

Invasive insects are known to present a threat to natural, agricultural, and urban systems, and while prevention is the best strategy, eradication following arrival might be considered a second-best option (Mack et al. 2000, Myers et al. 2000, Simberloff 2003, Brockerhoff et al. 2010). Simberloff (2003) provides a strong argument for the need to study the biology of

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invading organisms to inform eradication efforts, though he points out that this should not come at the price of delays that shrink the window of time in which eradication is feasible. Rapid eradication can reduce financial costs and the potential for non-target effects, while increasing the potential for success by taking advantage of small populations with limited distributions (Myers et al. 2000, Brockerhoff et al. 2010). However, speed in eradication can come with reduced opportunities to collect biological data on the invasive species, data which may benefit the improvement of eradication and management strategies (Mack et al. 2000, Simberloff 2003) in both current and future infestations.

The challenges created by these two priorities are evident in the efforts to eradicate the Asian longhorned beetle (*Anoplophora glabripennis*) in the United States. This beetle, which has also established populations in Canada, France, Germany, Italy, Austria, the United Kingdom, and the Netherlands, is a polyphagous wood borer of deciduous trees. Feeding and oviposition by females has been reported on at least 43 tree species (Hu et al. 2009, Haack et al. 2010) within 15 families, primarily in the genera *Acer*, *Populus*, *Salix*, and *Ulmus* (Lingafelter and Hoebeke 2002; Williams et al. 2004a; Wang et al. 2005). This broad host range combined with the beetle's ability to survive and emerge from untreated solid wood packing material used in international shipping (Bartell and Nair 2004; GAO 2006; Westphal et al. 2008) has made this species a global concern.

The first known infestations in North America were associated with urban environments near ports of entry (Chicago, IL, New York Metro Area, NY, and Jersey City, NJ) and surrounding areas (Nowak et al. 2001; Smith et al. 2009). Federal, state, and municipal efforts have led to declarations of eradication in Illinois (USDA 2008), New Jersey (NJDA 2013) and two boroughs and a town in New York (Manhattan, Staten Island, and Islip, respectively) (USDA 2013). Eradication has also recently been declared for the infestation in Boston, MA, where 6 infested trees were identified and removed (USDA 2014a). Eradication in these urban settings has been facilitated by the limited abundance and distribution of trees in managed, city maintained landscapes. In these environments where the density of hosts is low and connections to more densely wooded landscapes are limited, the ability of the beetle to expand its range may have been moderated.

The more recently detected infestations in Worcester, MA [2008] and Bethel, OH [2011] however present very different challenges to eradication, and highlight the need for both a rapid eradication response and a sound understanding of the behavior and biology of the invasive organism. These populations are established in heavily wooded suburban landscapes connected to contiguous tracks of the hardwood forests covering much of eastern North America. Based on the severity of this risk, the United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS), in collaboration with state and local governments and organizations have worked aggressively to remove and destroy infested material from the regulated areas. Since 2008, approximately 34,000 trees (both infested, and those deemed to be high-risk) have been removed and destroyed by chipping, and more than 5 million trees have been surveyed (USDA 2014b) in the Worcester, MA regulated area. While this rapid response has reduced beetle pressure in the infested area (Nehme et al. 2014), the need to focus resources on rapid survey and removal has not always allowed for the collection of highly detailed data describing the precise location and level of infestation of individual trees, or in situ studies of beetle behavior, information which is needed to identify patterns of spread and quantify risk to the surrounding landscape.

Like many invasive species, little data on dispersal and behavior was available to guide eradication programs prior to the beetle's identification as a species of concern. In its native ranges in China (Wu and Jiang 1998) and the Korean peninsula (Peng and Liu 1992; Lingafelter and Hoebeke 2002; Williams et al. 2004a) the beetle is not typically abundant in stands of mixed native trees, though outbreaks of Asian longhorned beetles (hereafter ALB) are known to occur in China in planted monocultures of preferred, non-native host trees (frequently North American poplars) (Hsiao 1982). Mark-and-recapture studies conducted in the beetles native range have provided a baseline of dispersal behavior and indicate 98 % of beetles disperse within 920 m of their point of release, with observed dispersal distances as high as 2600 m (Smith et al. 2001, 2004). While these studies provide much needed information on dispersal in the beetle's native range, little is known about dispersal in an invaded landscape where population densities are low and host availability is high. In an introduced environment, studies such as mark-and-recapture experiments or longitudinal life table investigations are often not feasible as recently established populations and populations under eradication may have low densities (Nehme et al. 2014). Similarly, the maintenance or release of healthy invasive organisms under eradication is typically considered antithetical to eradication efforts. Yet, there is a growing need to understand the dispersal dynamics, particularly in cases such as Worcester, MA, where widely distributed populations have the potential to expand into heavily forested landscapes.

In this study, we used records of infested trees documented by the USDA APHIS Plant Pest Quarantine (PPQ), Worcester, MA Asian Longhorned Beetle Eradication Program to reconstruct four potential patterns, or scenarios, of beetle spread in the invaded landscape. The four scenarios included two different assumptions (Strict and Relaxed) of the propensity of female beetles to disperse from their natal trees (representing a gap in current knowledge of beetle behavior in an infested area), and two data sets of varying completeness (representing the challenges typical of data collection in a large and rapidly evolving eradication program). Taking this flexible, large-scale approach can provide information needed to evaluate the potential for current and future beetle movement in the infested landscape. This approach can also provide an empirical basis for risk assessments and mitigation strategies while evaluating the potential role of “known-unknowns” for an invasive insect such as dispersal propensity.

Methods

Identification of infested trees

Female ALB chew oviposition pits on the trunk and branches of host trees where they deposit individual eggs. This chewing activity leaves distinctive wounds on the tree, and in combination with the exit holes left by emerging adults provides the indications of beetle activity used to visually identify infested trees.

Data sources

The data used in these analyses were generated by ongoing surveys conducted by Federal, State, and private contractor surveyors both from the ground using binoculars and spotting scopes, and from within the canopies by tree climbers and bucket truck operators. The survey is part of the Massachusetts Asian Longhorned Beetle Eradication Program, managed by the USDA Animal and Plant Health Inspection Service (APHIS), Plant Protection and Quarantine (PPQ) program, in collaboration with the Massachusetts Department of Conservation and Recreation (DCR) office established in Worcester, Massachusetts. When found, infested trees are assigned a unique program identification number and identified to genus and species (when possible). In addition, data documenting the diameter at breast height (dbh) and location of the trees are recorded. Prior to July 2010, tree locations were documented by recording the street address of the property on which the tree was located. Since then, the latitude and longitude of individual trees has been documented using hand-held GPS receivers. Between 2008 and 2011 data were warehoused in the APHIS Emergency Response Information System (ERIS) database. Since 2011 data has been documented in multiple databases (including continued use of ERIS) in order to facilitate data access and utility. The data analyzed are a compilation of available data from these databases as of 02/13/2014 and subjected to a QA/QC process as described below.

Data inclusion and quality assurance/quality control

Prior to analysis, the data used underwent a QA/QC procedure to identify errors and inconsistencies and to apply consistent criteria for data inclusion. Errors in the database typically came in one of three forms; (1) duplication (individual trees represented by multiple entries in the database), (2) consolidation (multiple trees represented by a single record), and (3) incomplete or illogical data attributes.

Duplicate tree records, which comprised the bulk of the database errors, were identified using attribute data including tree-id values and/or identifying records with matching location, dbh, and species information. Duplicate records were removed from the database. The database also included individual records which represented multiple trees. This compiling of individual trees was sometimes done in the early stages of the ALB Eradication Program when there was a strong emphasis on the rapid removal of trees, and these data points tended to be clustered around the core of the infestation where the first infested trees and stands were identified and removed. These records were identified using the dbh values, as the diameters for the removed trees were combined, resulting in single "tree" records with dbh values as high as 6896 cm. Tree records with dbh values greater than 127 cm were individually flagged and evaluated to determine whether the records represented large individual trees or multiple trees combined into a single record. The use of 127 cm (=50 inch) as a filter value was recommended by field surveyors involved in the data collection.

Errors of the third type included records with missing or illogical information on the location, species, and the level of infestation in the tree. In cases where the source of the error was readily identifiable (for example, the transposition of the first two digits of a latitude value), the data were repaired. The most common database error was missing information on the level of infestation within the tree; these records were also typically from the early stages of the ALB Eradication Program. These records were assigned an infestation level of "U" (Unknown) and were analyzed as described below. In cases where the location data could not be repaired unambiguously, the tree records were removed from the database. The application of the QA/QC process yielded a data set with records for 15,053 infested trees within the 284 km^2 regulated area from an original report generating 22,784 records, with duplicate data entries making up the bulk of the filtered records.

Beetle infestation levels

The level of beetle infestation within a tree is determined based on the type and quantity of visible oviposition pits and emergence holes left by adult beetles. Infestation levels are defined as A trees, containing female oviposition marks (but no emergence holes), B trees with 1–10 emergence holes, C trees with 11–100 emergence holes, and D trees with >100 emergence holes. The most heavily infested tree located in Worcester, MA was located near a holding site for industrial wood packing material and is assumed to be the original epicenter of the infestation. Within these analyses this tree is denoted as the "O" (Origin) tree (see insets on Fig. 1). The O tree was found to have >400 emergence holes and dating of emergence scars indicates the tree had been infested since at least 1998 (A. Sawyer, unpublished data). No beetle damage predating this time period has been found in the regulated area.

Tree adjacency scenarios and assumptions of beetle dispersal behavior

Graph theory is an approach to the study of how objects, often called nodes, are distributed and connected using graphical representations. In this context the nodes represent individual trees, and the movement of beetles between trees defines which trees are connected. These connections are represented graphically by lines connecting the nodes and are referred to as edges or adjacencies. Here, we built four scenarios or sets of adjacencies by varying two parameters, each applied with one of two conditions. The first varied parameter was the quality and completeness of the data included in the analyses. Early in the eradication process (primarily the infested trees detected in 2009), ~7500 infested trees were identified and removed without documenting the level of infestation. As previously described, these trees are included in the database as U level trees. To estimate the impact of this missing information on inferred patterns of beetle dispersal, the analyses were conducted both with (U Inclusive, ~15,000 trees total) and without (U Exclusive, ~7500 trees total) these trees. The analyses which include U trees are based on the assumption that the trees were A level infestations, as even in the early period of the eradication program trees with substantial infestations were frequently documented in greater detail.

The second variable assumption in the scenarios is the presumed dispersal propensity of adult female beetles. Within this study the abundance of beetles (infestation level) is assumed to be a correlate of the age of the infestation within a tree, such that the initiation of infestations in D trees predates the infestation of C trees, C trees predate B trees, etc. However, it is not assumed that all trees can serve as sources of dispersing adults. Previous reports have suggested females typically remain on their natal tree when resources are still available (Sawyer 2009). As such, A trees, which lack emergence holes, and B trees, with very few emergence holes may rarely act as source trees, while heavily infested C and D trees may

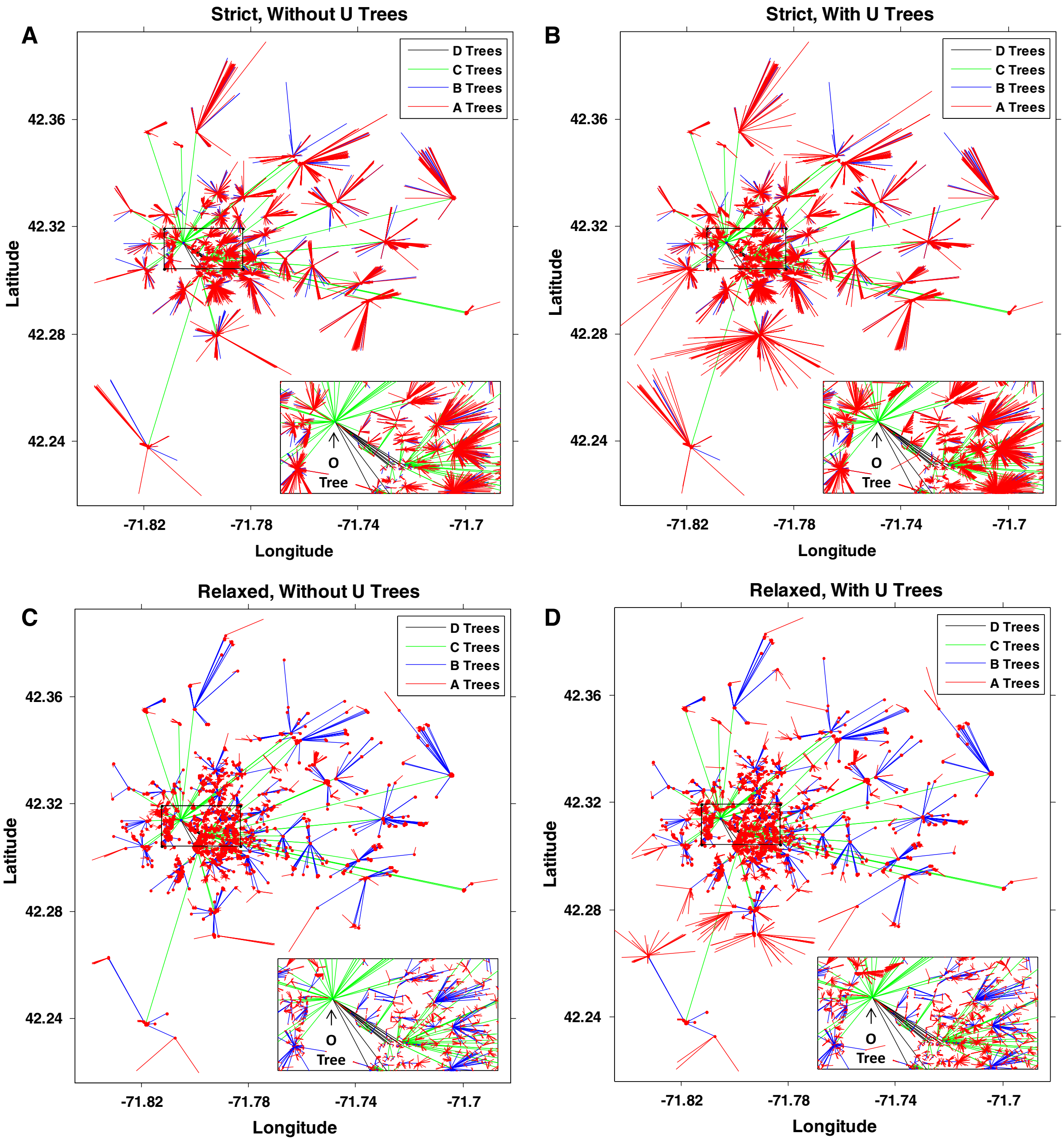

Fig. 1 a–d Adjacency graphs depicting the inferred dispersal of ALB among trees in the greater Worcester, MA area using two beetle dispersal scenarios (Strict and Relaxed), with and without trees with incomplete data records (U trees). **a** Strict dispersal assumptions without U trees, **b** Strict dispersal assumptions with U trees, **c** Relaxed dispersal assumptions without U trees, **d** Relaxed dispersal assumptions with U trees

more frequently generate emigrants. Unfortunately studies quantifying the propagule pressure exerted by a tree as a function of the level of infestation within the tree are not available. To accommodate this knowledge gap we have bracketed this aspect of dispersal by evaluating beetle movement (analyzed as tree adjacency) for two scenarios based on “Strict” and “Relaxed” dispersal assumptions.

Under the Strict dispersal assumption it is assumed that beetles do not readily disperse from lightly infested trees. Therefore, A and B trees may not serve as sources of infestation, and are assumed to have been infested by beetles originating from the nearest C or D tree. Under the Relaxed dispersal assumption, this limitation to dispersal is removed and beetles are assumed to readily disperse from any tree with exit holes, allowing B trees (in addition to C and D trees) to serve as the source of beetles for infestations in nearby A trees. The O tree was removed in 2008, and so could not serve as the source for beetles to produce the fresh oviposition pits found on A trees, though it was assumed to serve as a potential infestation source for older establishment events (B, C, and D trees).

This approach simplifies the analysis by assuming that adjacencies (vectors of movement on the landscape) represent the movements of individual beetles, which provides an empirically generated dispersal kernel. However, this approach does not incorporate time explicitly, and as such does not directly measure the rate of spread. While the generalized rate of spread for the infestation could be estimated by the distance between the assumed epicenter of the infestation and the distal-most infested tree, divided by the number of years of beetle presence, these analyses are not included within this study for two reasons. First, this approach would assume that the distal infestations are the result of evenly spaced and timed dispersal events, an assumption that may not be biologically valid and which does not capture the variation in dispersal distance described by the dispersal kernel. Second, conducting these analyses on a landscape scale would require the dendrochronological dating of the infestation of multiple, distal trees in order to generate a population of rates to estimate the general rate of spread. Unfortunately, this scale of dendrochronological data is not currently available. Dendrochronological studies are under way for sub-sections of the population (Trotter and Hull-Sanders, unpublished data) in an effort to develop an analysis of spatial and temporal patterns of beetle spread at the scale of individual stands, though the spatial scale remains limited.

Adjacency rules

Beetle movement from one tree to another is defined in this analysis by tree adjacency (connections between trees). Adjacency among trees was identified based on two rules: (1) Trees receive beetles from (and are therefore adjacent to) the nearest tree with an older infestation (using either the Strict or Relaxed dispersal assumptions) and (2) trees may act as the source of infestation for multiple trees, but are assumed to have been infested only once. Tree adjacency lists for each of the scenarios were generated using the NEAR function in ArcMap (ESRI ArcMap V 10.0). These lists were then converted to adjacency matrices to generate adjacency graphs. The lengths, distributions, and percentiles of these inferred dispersal events (adjacency vectors) were calculated using a custom built script (ALBtreeadjacency.m) in MatLab (MatLab Release 2013b v8.2.0.701). Distance vectors were tabulated to produce curves of vector length by frequency, which in turn were used as an empirically generated dispersal kernel for the Asian longhorned beetle in Worcester, MA.

Results

Inclusion/exclusion of U trees

The empirical dispersal kernel for the Asian longhorned beetle in Worcester, MA varied with the inclusion or exclusion of the U trees, and under scenarios with Strict and Relaxed dispersal assumptions (Table 1 and Figs. 1a–d, 2, 3). The inclusion or exclusion of U trees makes a difference in the density of vectors (contrast Fig. 1a with 1b, and 1c with 1d) within the infested landscape, but does not alter the overall spatial distribution of infested trees. Because the inclusion of the U trees approximately doubles the number of trees included in the same area, it would be expected that the average distance between points (assuming a generally random distribution of points on the landscape) would decrease. Accordingly (and as Fig. 2 shows) including the U trees changes the curve in both scenarios, with a general reduction in the median dispersal distance (Table 1).

Strict versus Relaxed dispersal assumptions

Changes in the assumptions of beetle dispersal (i.e. Strict vs. Relaxed) made a substantial difference in the spatial pattern of dispersal vectors, as shown by comparison of Fig. 1a with 1c, and 1b with 1d. The effect of imposing Strict rules on dispersal limits the

Table 1 Quantile dispersal distances (m) based on Strict and Relaxed assumptions of dispersal propensity, and with and without the inclusion of U trees

Dispersal assumption	Incl. U trees	50th percentile distance (m)	90th percentile distance (m)	95th percentile distance (m)	98th percentile distance (m)	99th percentile distance (m)	99.9th percentile distance (m)
Strict	No	234	1013	1400	2098	2979	4935
	Yes	195	832	1178	1980	2382	4639
Relaxed	No	37	300	594	1138	1719	4935
	Yes	39	232	422	933	1358	4639

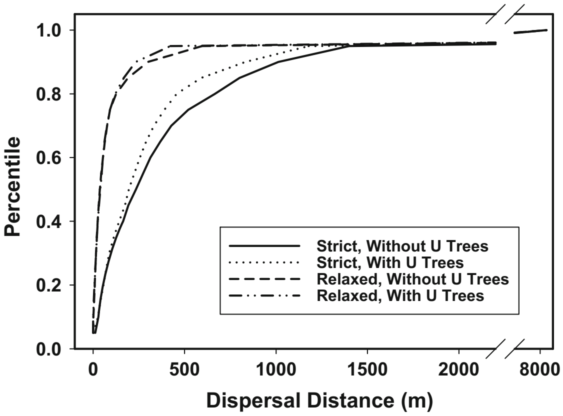

Fig. 2 The *curves* show the accumulation of dispersal events by distance under the two scenarios (Strict and Relaxed), and both with and without the inclusion of U trees

sources of dispersal to those trees which have higher abundances of beetles, trees which are also less common on the landscape. Like the change in the number of total trees in the analysis, the Strict scenario reduces the abundance of source points on the landscape and so increases the median inter-point distances relative to the Relaxed scenario, as shown by the curves in Fig. 2. While both of these factors (data completeness and beetle behavior) impacted the inferred dispersal distance probabilities, changes in beetle behavior yielded the longest dispersal distances, suggesting it plays a major role in identifying the risk to the surrounding landscape.

Discussion

Effective eradication programs for invasive species can benefit from strategies driven by the biology and ecology of the target organism, though data collection opportunities may be limited when the management priority is rapid eradication. Here, using data collected by the USDA APHIS PPQ ALB Eradication Program in Worcester, MA, we have generated four empirical estimates of the Asian longhorned beetle dispersal kernel in an invaded landscape. These four dispersal distance probability curves capture variation driven by two scenarios of beetle dispersal behavior (which recognize a gap in biological knowledge of the species) and two databases with differing levels of data quantity. These data suggest that it is possible to quantify patterns of spread in the beetle, even with limited data. Further, these results suggest that, at least in this case, incomplete data (represented by the removal of U trees from the analyses) resulted in changes in the estimated dispersal kernel which were smaller than the impact of changing assumptions of dispersal behavior.

The assumption of strict dispersal rules (i.e. beetles do not leave their natal tree until the tree is heavily utilized) produced the longest dispersal distances, with a 99th percentile dispersal distance of over 2.3 km (Table 1). Under the relaxed scenario, in which it is assumed that all infested trees can act as sources for dispersing beetles, the 99th percentile distance was reduced by more than 1 km (note that for these discussions, the values being compared are derived from the more complete dataset which includes the U trees). The determination of which set of dispersal assumptions is most appropriate will require more detailed evaluations of the behavior and biology of beetles in the field. Direct measures of dispersal in an invaded landscape would necessitate methods such as mark-and-recapture, or large-scale tracking of individuals using radio tags (see Williams et al. 2004b), methods which are not compatible with eradication

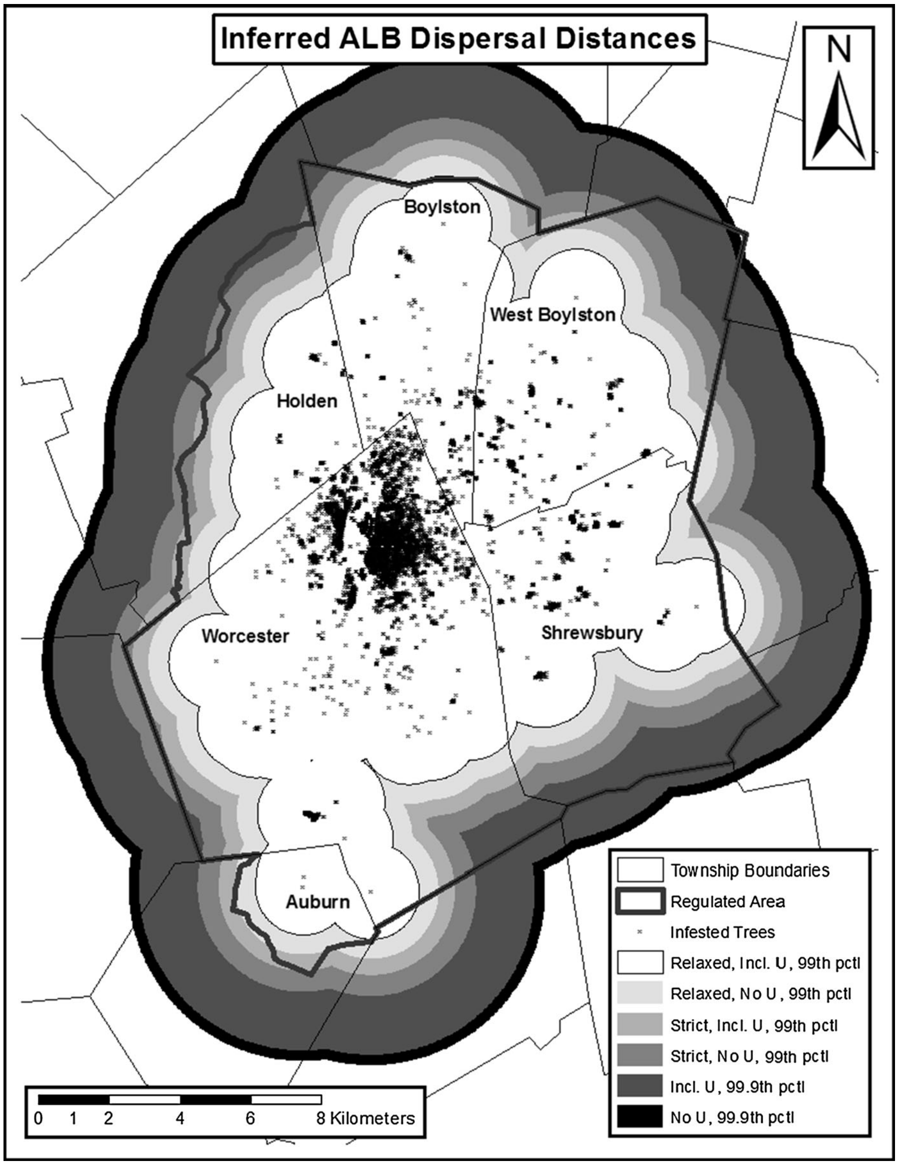

Fig. 3 Locations of 99th and 99.9th percentile dispersal distances under Strict and Relaxed assumptions, because the locations of the boundaries with and without U trees differs by only 4 m for the 99.9th percentile distances, only the distance with U trees is shown

efforts. While this limits opportunities to quantitatively evaluate the goodness of fit between these inferred patterns of beetle movement and the true pattern of dispersal on the landscape, a previous study by Smith et al. (2004) using a mark-and-recapture method found that in the beetle's native environment, 98 % of beetles dispersed at distances of 920 m or less. Although Smith et al. (2004) cautioned that these patterns might differ from those found in an invaded landscape, it is interesting that the results from the best-case scenario (i.e. the Relaxed scenario which generated the shortest dispersal distances) yielded a remarkably similar 98th percentile distance of 933 m, despite the use of different analytical approaches in different landscapes.

While the inferred dispersal distances of the Relaxed scenarios are in agreement with the patterns described by Smith et al. (2004), the data from the Worcester ALB infestation also suggest that more rare dispersal events such as those in the 99.9th percentile may be as long as 8 km. These rare events may be influenced by extrinsic factors such as the transport of

Table 2 Summary of assumptions and implications of inferred ALB dispersal behavior in Worcester, MA

	Strict	Relaxed
Assumptions		
Dispersal propensity	Do not readily disperse	Readily disperse
Population pressure	High	Low
Host Resource	Over-utilized	Under-utilized
Implications		
Dispersal distance	Long	Short
Host source	O, D, and C level trees	O, D, C, and B level trees

infested firewood and beetles "hitchhiking" on vehicles, or may be the result of rare naturally occurring long-distance dispersal events by individual beetles. Given the findings by Smith et al. (2004) who documented dispersal distances as long as 2600 m using mark-recapture methods, an approach in which it is often difficult to detect rare long-distance dispersal events, the potential for beetles to move these long distances under their own power cannot be eliminated. The agreement between the findings of Smith et al. (2004), and the inference based approach described here suggests that applying both methods in combination may be an effective approach to developing robust estimations of dispersal kernels for an invasive species.

Previously it has been assumed that Asian longhorned beetles behave in accordance with the Strict scenario, and as such are typically slow to disperse, remaining on the natal tree until the resources in the tree decline (Sawyer 2009). Interestingly, while this scenario implies fewer sources of dispersing beetles on the landscape, the reduced density of source trees results in an increased inter-tree dispersal distance. Consequently, the assumption that the beetle is slow to disperse implies that when dispersal events do occur, they occur over longer distances. Conversely, the assumption that beetles disperse readily allows for an increase in the number of trees that can serve as beetle sources. Because the overall area of analysis does not change, the increased density of potential beetle sources results in a reduction in the median inter-tree distance (Table 1). Thus, under the Relaxed scenario more trees act as a source of beetles, but the typical dispersal distance is shorter.

While the central portion of the cumulative dispersal-distance curve is influenced by the assumptions of adjacency (i.e. which trees are connected), changes in the assumptions of adjacency have a limited impact on the 99th, and 99.9th percentile dispersal distances (Table 1). Within these results, the longest dispersal distances are assumed to have occurred early in the infestation, between the O and D trees (though the reasons for this remain unknown), and these dispersal events are unaffected by differences between the Strict and Relaxed dispersal scenarios. As a consequence, within the context of identifying the locations of the high percentile boundaries (Fig. 3), the distinction between the two scenarios may not be critical.

Mitigation strategies under Strict and Relaxed scenarios

While the impact of dispersal behavior on the determination of the 99th and 99.9th percentile boundaries was limited, the differences between the two scenarios imply differences in dispersal sources and distances, both of which could play a role in the development of ALB eradication strategies (Table 2). Under the Strict scenario, in which dispersal events are longer in distance but are limited to originating from trees with high infestations, the spread of the population might be controlled by rapidly identifying and removing highly infested trees (the sources of long-distance dispersing beetles). The removal of these trees could in turn reduce the risk of spread and allow additional time to identify and remove the more difficult-to-find lightly infested trees. Assuming a gradient of infestation intensity that decreases with distance from the epicenter of the invasion (the O tree), tree removals might start near the center of the infestation and progress outwards towards the lightly infested edges of the population.

This approach would contrast with one that might capitalize on beetles behaving in accordance with the Relaxed scenario. In this scenario low density populations produce dispersing individuals which travel shorter distances (though from a larger number of sources). As a result, dispersing individuals which contribute to range expansion would be likely to originate near the edge of the population. Under these conditions, delineating the edges of the infestation becomes a high priority, as efforts to limit spread would benefit from the removal of infested trees at the perimeter of the infestation, with tree removals progressing back towards the center. The need to fill this knowledge gap is in alignment with the assertion by Mack et al. (2000) that successful eradication is strongly influenced by three factors, the first of which is the matching of the biology of the organism to the tools and strategies used to eradicate it. Work also remains to identify links between the biology and behavior of the beetle and its distribution relative to landscape variables such as those described by Shatz et al. (2013), and to parameterize mathematically driven models of beetle spread (Gourley and Lou 2014).

This analytical approach may also have uses for other invasive species which leave a record of both the timing and intensity of infestations in the wood of trees, such as the Goldspotted Oak borer (*Agrilus auroguttatus*) in California (Lopez et al. 2014) and Emerald Ash borer (*Agrilus planipennis*) (Siegert et al. 2014). The continued collection of data by eradication and management programs, along with improvements in data quality and accessibility can provide opportunities to refine these estimates and expand the development of these tools which both improve our understanding of invasive species dynamics, and our understanding of how to manage invasive species populations at a landscape scale. Given the financial and ecological costs associated with invasive species (Pimental et al. 2000, 2001, 2005), the need for these tools is likely to continue.

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