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BIODIVERSITY RESEARCH

# Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America

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## ABSTRACT

Limiting the damage by non-indigenous species requires rapid determination of current and potential distributions and vectors of dispersal, and development of appropriate management measures. The emerald ash borer (*Agrilus planipennis*), a wood-boring beetle native to South-East Asia, was first reported in the Great Lakes region during summer 2002. The beetle poses an enormous threat to native ash (*Fraxinus*) species of North America, as untreated trees in infested areas of Ontario, Michigan and Ohio suffer high mortality. We demonstrate that the borer has spread in North America through a combination of diffusive range extension, associated with local flights, and by long-distance 'jump' dispersal associated with human movement of infested sapling or contaminated firewood. Probability of infestation was inversely related to distance from borer epicentres but positively related to the size of human population centres. At least 9 of 39 populations that were first reported in Michigan during 2004 cannot be accounted for by local diffusion, raising the possibility that other unidentified mechanisms may be contributing to the dispersal of the beetle. In the absence of quarantine, by 2005 all of Michigan's lower peninsula was contained within the boundaries of potential diffusive range expansion. Infested ash saplings also were introduced from Michigan to Maryland during 2003, and subsequently transplanted to five sites in Maryland and Virginia. Quarantine and eradication measures have had mixed results: in the south-central USA, the species appears on the brink of eradication, whereas its distribution has continued to spread during 2005 in the Great Lakes region despite extensive containment and quarantine measures. Quarantine success in the Great Lakes region is encumbered by multiple dispersal vectors, larger borer population sizes and by the more extensive geographical distribution that was achieved prior to implementation of control measures.

### Keywords

**Dispersal kernel, gravity model, Great Lakes, invasive, non-indigenous species, stratified dispersal.**

## INTRODUCTION

Dispersal is fundamental to species distributions and ecology. With a history that dates back to Darwin, dispersal remains one of the most intensively studied fields in ecology (e.g. Clobert *et al*., 2001; Bullock *et al*., 2002; Nathan, 2005). In recent years, attention has focused on the relative contributions of local and long-distance dispersal and their consequences for species ranges, patterns of dispersal and population persistence (e.g. Lewis, 1997; Higgins & Richardson, 1999; Levin *et al*., 2003; Green & Figuerola, 2005; Trakhtenbrot *et al*., 2005). Biological invasions by non-indigenous species represent an important applied extension of dispersal ecology since, in many cases, human-mediated dispersal transports a significant number of individuals to distances farther from the source than they could disperse naturally (e.g. Hebert & Cristescu, 2002). As with their counterparts in basic ecology, invasion biologists have focused on the relative importance of local vs. long-distance dispersal (With, 2002, 2004; Neubert & Parker, 2004; Hastings *et al*., 2005; Puth & Post, 2005). Long-distance dispersants provide opportunities for 'nascent foci' to develop, from which new populations or coalescing nodes can be founded (Moody & Mack, 1988; Lewis, 1997; Muirhead & MacIsaac, 2005). The choice of control strategies (e.g. suppression, containment, eradication) is, in turn, affected by the dispersal characteristics and geographical distribution of the species in relation to funding available for management (Moody & Mack, 1988; Sharov, 2004; Taylor & Hastings, 2004).

The International Union for Conservation of Nature and Natural Resources' Global Invasive Species Database compilation of the world's 100 most harmful, non-indigenous species includes 14 insects (Lowe *et al.*, 2000). Considering that insect invasions can have profound consequences to human, animal, plant and ecosystem and economic health, it is not surprising that their dispersal characteristics and population ecology have been well studied (e.g. Gilbert *et al.*, 2003, 2004; Krushelnycky *et al.*, 2004; Morrison *et al.*, 2004; Smith *et al.*, 2004; Juliano & Lounibos, 2005). The emerald ash borer (borer) is a beetle native to South-East Asia, including parts of China, Korea, Japan, Russia, Mongolia and Taiwan (Liu *et al.*, 2003). The borer was first observed in south-eastern Michigan and south-western Ontario (Fig. 1a) in summer 2002, following investigations of dieback and epicormic branching in native ash species. The borer likely entered North America in infested ash strapping, pallets or dunnage more than 10 years ago (Herms *et al.*, 2004). Adults lay eggs under tree bark, and the feeding larvae kill trees by disrupting nutrient transport in the phloem (Liu *et al.*, 2003). Affected species include green ash (*Fraxinus pennsylvanica*), white ash (*Fraxinus americana*), black ash (*Fraxinus nigra*) and blue ash (*Fraxinus quadrangulata*) (Liu *et al.*, 2003). Collectively, these species are a dominant component of the eastern deciduous forest of North America, a status now threatened by spread of the borer. The borer also threatens about $300 billion of timberlands in the USA (Nowak, 2003).

Adult dispersal by flight is strongly gender-biased, with a mode of 0.8 km in 24 h per individual female, and only 1% travel farther than 4 km (Taylor *et al.*, 2004). Larval beetles can be transported over long distances in contaminated nursery stock, firewood or raw logs. The combination of local, natural dispersal of adults and human-mediated long-distance

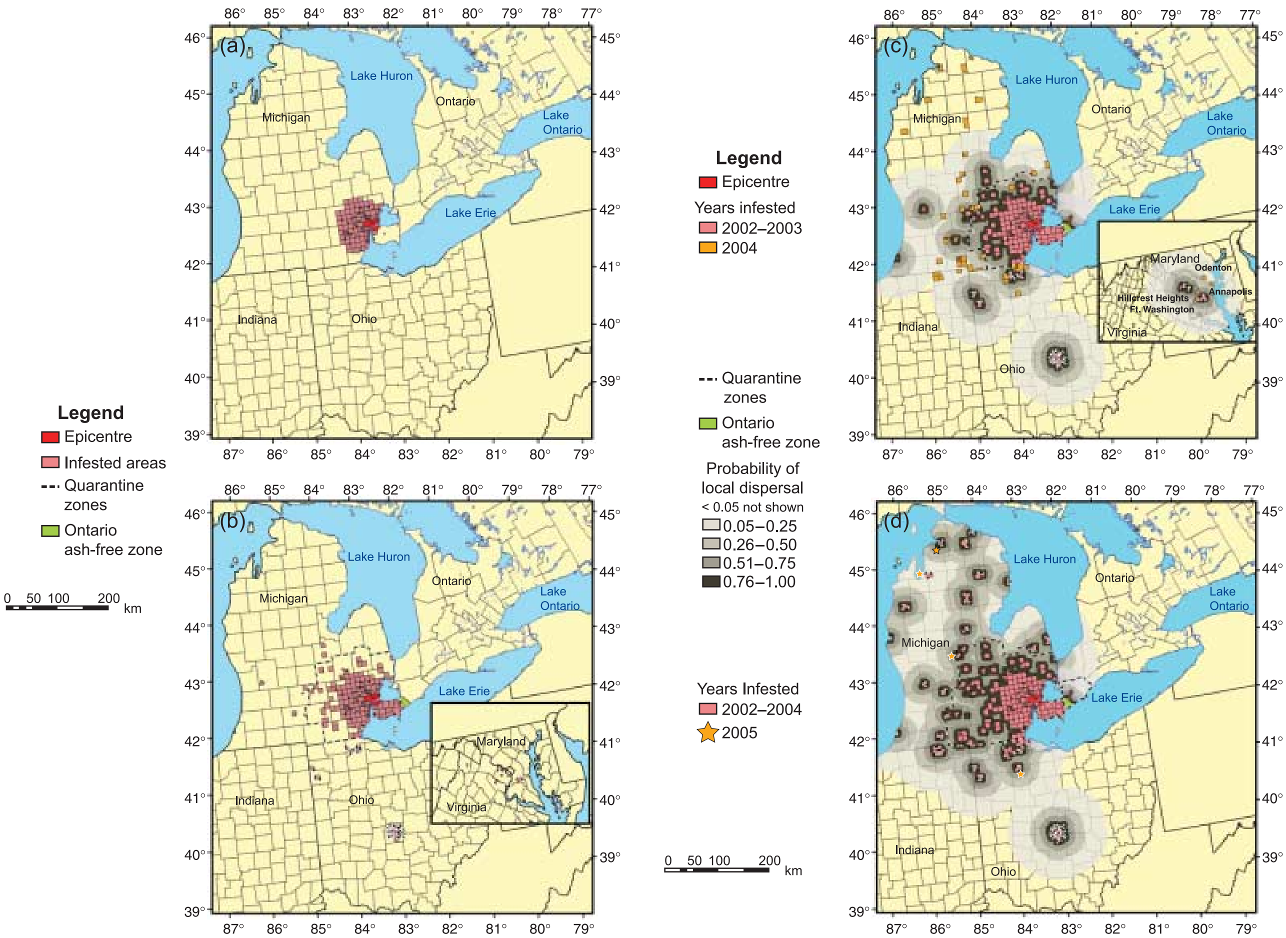


Figure 1 Sightings of the emerald ash borer from 2002 (a), 2003 (b), 2004 (c) and 2005 (d) in the USA and Canada, and predicted local dispersal of the beetle *via* adult beetle flights from infested areas in 2002–03 (c) and 2002–04 (d). Local dispersal is based on an exponential decay function (probability of spread = $e^{-bx*D}$, where b is 0.038 for the USA and 0.050 for Ontario, and X is distance from the centre of the invasion source in km). An ash-free 'firewall' (light green) was cut in Ontario during winter 2003/2004 to reduce the probability of locally dispersing beetles settling in areas with uninfested ash hosts. The epicentre of the invasion in SE Michigan and SW Ontario is shown in red and quarantine zones are outlined with a dashed black and white line.

transport of larvae is consistent with stratified diffusion (see Hengeveld, 1989). Other non-indigenous species that spread via stratified dispersal include molluscs (Bossenbroek *et al.*, 2001), other insects (Sharov *et al.*, 2002; Gilbert *et al.*, 2003) and plants (Higgins *et al.*, 2003). Establishment of satellite colonies rapidly increases the overall rate of spread and area infested (Moody & Mack, 1988; Lewis, 1997) and increases the complexity of management decisions. In this paper, we explore dispersal patterns of the borer from its first detection through to spring 2005. We develop a stratified diffusion model that incorporates local and long-distance transport to project dispersal of the species.

## METHODS

We obtained records of first reporting of the borer for the USA and Canada from the Michigan, Ohio, Indiana and Maryland Departments of Agriculture and the Canadian Food Inspection Agency. We used three approaches to predict local and long-distance dispersal of the borer. First, we modelled local diffusion based on changes in the reported distribution of the infested subcounties (i.e. township or municipality) using a standard exponential decay function, relating the probability of dispersers stopping at a given destination and distance from the epicentre to the centroids of infested and non-infested areas in 2002, and from 2002 sources to sites reported invaded during 2003 (see Lewis, 1997). This function was used to predict occurrence in 2004 and the same function was then used to predict the 2005 distribution from 2002 to 2004 infestations. This model is phenomenological in that it makes no assumptions about flight capabilities of the borer, although it implicitly assumes dispersal occurs via adult flights.

The probability ($P_j$) of a destination remaining non-infested is given by the joint probability that the borer fails to disperse from all infested subcounties $i$ to destination $j$:

$$P_j = \prod_i \left[1 - \frac{\exp(-bx_{ij})}{d_i}\right] \tag{1}$$

where $b$ is the estimated coefficient of the exponential slope, and $x_{ij}$ is the Euclidean distance from source ($i$) to non-infested destination ($j$), estimated as the centre of each subcounty. $d_i$ is a normalizing constant given by:

$$d_i = \sum \exp(-bx_{ij}) \tag{2}$$

where $d_i$ scales for all potential destinations, such that $P_j$ ranges from 0 to 1, and we obtain the relative risk of invasion. The slope of the exponential kernel, $b$, is solved by finding the minimum value of the likelihood function, $L$, where:

$$L = \begin{cases} -\sum_{j=1}^{m} \log(1 - P_j), \ j \text{ is invaded} \\ -\sum_{j=1}^{m} \log(P_j), \text{ otherwise.} \end{cases} \tag{3}$$

Slopes of the exponential decay functions were calculated separately for the USA and Ontario, Canada owing to the smaller spatial scale of township divisions in the former. Predicted areas of local dispersal were mapped in an Albers Equal-Area Conic projection to maintain the shape and distance between infested areas using ARCGIS (Desktop version 8.3, ESRI, Redmonds, CA, USA).

Second, we predicted long-distance dispersal of the borer under two scenarios of human-mediated transport. First, long-distance dispersal of the borer was modelled based on human population size at the subcounty level using the US 2000 Census and beetle invasion status. Models based on population size at this spatial scale were constructed only for Michigan, Indiana and Ohio. We used population size of townships and municipalities as surrogates of human activities (e.g. horticultural ash trees) that may result in transfer of ash products from infested sources to non-infested destinations. Previously, human population density was found to provide the best estimate of spread of the chestnut leafminer moth *Cameraria ohridella* in Europe (Gilbert *et al.*, 2004). Comparable predictions of long-distance dispersal based on population size in Ontario were not possible, because required data from outlying centres are lacking. Data on invasion status, population size and distance from the epicentre for the three states were randomly divided into two 80: 20 training/model validation subsets. A spatial 'null' logistic regression model based on invasion status as a function of the log-transformed distance from the epicentre was constructed since reports of the borer are highly concentrated at the epicentre of the invasion, and the borer may not have had sufficient time to disperse throughout the three states. A second logistic regression model predicted the probability of invasion with a term added for log-transformed population size of the recipient area, and differences in fit between the two models were thus attributed to human population size. Validation of the second model was assessed by comparing the predictions of the test data subset fitted with the training model parameters to the observed invasion status of the testing data set. We used the generalized linear models in STATISTICA (version 7, Statsoft Inc., Tulsa, OK, USA) for model construction and validation.

Third, we developed a gravity model that utilized data pertaining to human-dispersed firewood to predict long-distance dispersal in Michigan, Ohio, Indiana and Ontario. Gravity models relate the interaction strength between a discrete, invaded source and a non-invaded destination, weighted by the distance between them, in a manner analogous to Newton's Law of Gravitation (Bossenbroek *et al.*, 2001; Muirhead & MacIsaac, 2005). In summer 2003, provincial and national parks throughout Ontario initiated a surveillance program to intercept firewood bundles brought by campers from within the quarantine zone. The number of wood bundles intercepted was related to the number of campsites as an independent measure of attractiveness, giving:

$$w = \alpha c d^{-\beta} \tag{4}$$

where $w$ is the number of wood bundles, $c$ is the number of campsites, and $d$ is the shortest road distance from the park to Windsor, Ontario, the invasion's Canadian epicentre. The unknown variables $\alpha$ and $\beta$ were simulated by fitting a nonlinear model using least-squares regression in STATISTICA (version 6, StatSoft Inc.). Road distance is preferable to straight-line distance from the parks to the quarantine zones as it reflects the actual distance covered by vehicles. We assume that the relationship among transported wood bundles and attractiveness to recreational parks developed for Ontario also hold for traffic to state parks in the USA. Ash trees are floristic dominants in both Canadian and American epicentres, and we assume the likelihood of transfer outside of quarantine areas was the same in both countries. The predicted number of wood bundles transported outside state and Ontario parks was interpolated by fitting an inversely distance-weighted surface to point data from the gravity model.

## RESULTS

### Emerald ash borer spread and quarantine

The beetle's invasion epicentre in North America encompasses the immediate area around Detroit, Michigan and Windsor, Ontario (Fig. 1a). Quarantine zones were established in 2002 in both Michigan (6 counties) and Ontario (1 county) in an attempt to prevent long-distance dispersal of the borer (Fig. 1b).

During 2003, the borer was reported in 13 townships in Michigan contiguous to sites reported infested during 2002 (Fig. 1a). These sites were all located within the quarantine zone, which had now expanded to 13 counties. The borer was reported at an additional six sites in Michigan outside of the newly established quarantine region. One of these sites, St. Joseph, located in Michigan's south-west corner, is almost 200 km from the nearest population identified in 2002. In Michigan, quarantine consisted of cutting healthy ash trees in the area immediately surrounding infestations, and banning export of ash products to non-infested regions. In Ohio, the borer was reported from six sites in three areas, with the farthest, Columbus, located 250 km from the nearest site reported invaded during 2002. Quarantine was established for all invaded sites in Ohio in 2003. In Ontario, the borer expanded its distribution to contiguous sites in Essex County (Fig. 1b), which was then placed under quarantine during summer 2003. In addition, a 10-km wide 'firewall' was created during winter 2003/2004 by cutting all healthy ash trees on public and private lands along the eastern boundary of the quarantine zone, between Lakes Erie and St. Clair, followed by chipping or burning of the cuttings (see Fig. 1b). This procedure was implemented to create a host-free (i.e. ash-free) region to slow spread to uninfested areas by flying adults. The borer also dispersed to Maryland and Virginia during 2003 (Fig. 1b). A tree nursery in Maryland received an illegal shipment of 121 infested saplings from within the quarantine zone in Michigan during April 2003, of which some were subsequently planted at one site in Virginia and four sites in Maryland.

The borer's distribution expanded dramatically in 2004. In Michigan, the borer was reported at one site inside the 2003 quarantine zone, eight sites outside but proximate (< 25 km) to it, and at 20 sites distal to the zone, including one location *c.* 225 km from the nearest known population (Fig. 1c). Seven new locations were reported invaded in Ohio during 2004, all in close (< 50 km) proximity to populations reported during 2003. New populations all were located in the NW part of the state, adjacent to infested areas in Michigan. The borer also spread to four locations in Indiana, all of which were ≥ 100 km from known infested sites. All newly discovered populations in the Great Lakes states were quarantined during 2004. Also, individual borers were reported at four sites in Maryland, which implemented quarantine efforts in spring 2004. These efforts consisted of destruction of all ash trees in the infested nursery, and on public and private lands in a surrounding 0.5-mile buffer zone. In total, almost 1000 infested or potentially infested trees were destroyed. The four new infestations were also eradicated (Fig. 1c). In Ontario, 23 new sites were reported invaded, all located within two foci on the distal side of the firewall. These trees were removed, and the quarantine zone expanded to nearly double its previous size (Fig. 1d).

Thus far, four new sites have been reported invaded during 2005. Three sites are located in Michigan, one straddling the 2004 quarantine perimeter, the other two along the north-eastern coast of Lake Michigan (Fig. 1d). The single report of invasion in Ohio during 2005 occurred at a site contiguous to one reported invaded during 2004, and is consistent with diffusive spread.

### Dispersal models

Distribution changes between 2002 and 2003 were used to develop a local, diffusion-based dispersal model. The area covered by the most expansive model, which considered invasion probabilities as low as 0.05, encompassed 77% of all sites reported invaded during 2004 in the Great Lakes states, though this value fell to 23% when the least inclusive model was used (i.e. 0.76–1.00 probability of invasion) (Table 1). If control efforts were not implemented, or if they prove unsuccessful, the range vulnerable to invasion by the borer in 2005 includes all of Michigan's lower peninsula. While the 23 occurrences observed east of the firewall in Ontario during 2004 are consistent with diffusive spread from across the firewall (i.e. $P = 0.26$), they are likely the result of firewood and saw logs transported prior to establishment of the firewall (K. Marchant, unpublished data). Likewise, dispersal of the borer within Maryland during 2004, although consistent with diffusive spread $P = 0.51$), was the result of movement of infested saplings within the state.

The logistic regression model predicted dispersal based on distance from the epicentre and human population in the recipient area (Fig. 2a). The addition of the human population term improved the model fit significantly over the null model based only on distance from the epicentre ($\chi^2 = 16.52$, d.f. = 1, $P < 0.0001$), implying that human population size (in recipient areas) and activity is a major factor in the spread of the borer. The long-distance invasion probability for Michigan, Ohio and Indiana was estimated as:

$$P(\text{infestation}) = \frac{\exp(7.95 - 2.92d + 0.37n)}{1 + \exp(7.95 - 2.92d + 0.37n)}$$

**Table 1** Cumulative number of infested townships and municipalities inside (or contiguous to) and outside of zones categorized by probability of local diffusion for the Great Lake states. The probability model is based on range expansion that occurred from 2002 to 2003 (for 2004 predictions) and 2002 through 2004 (for 2005 predictions)

| | Year | | | |
|---|---|---|---|---|
| | 2004 | | 2005 | |
| Probability of dispersal | Number of new invasions inside the probability zone | Number of new invasions outside the probability zone | Number of new invasions inside the probability zone | Number of new invasions outside the probability zone |
| 0.05–0.25 | 30 | 9 | 4 | 0 |
| 0.26–0.50 | 21 | 18 | 4 | 0 |
| 0.51–0.75 | 10 | 29 | 4 | 0 |
| 0.76–1.00 | 9 | 30 | 4 | 0 |

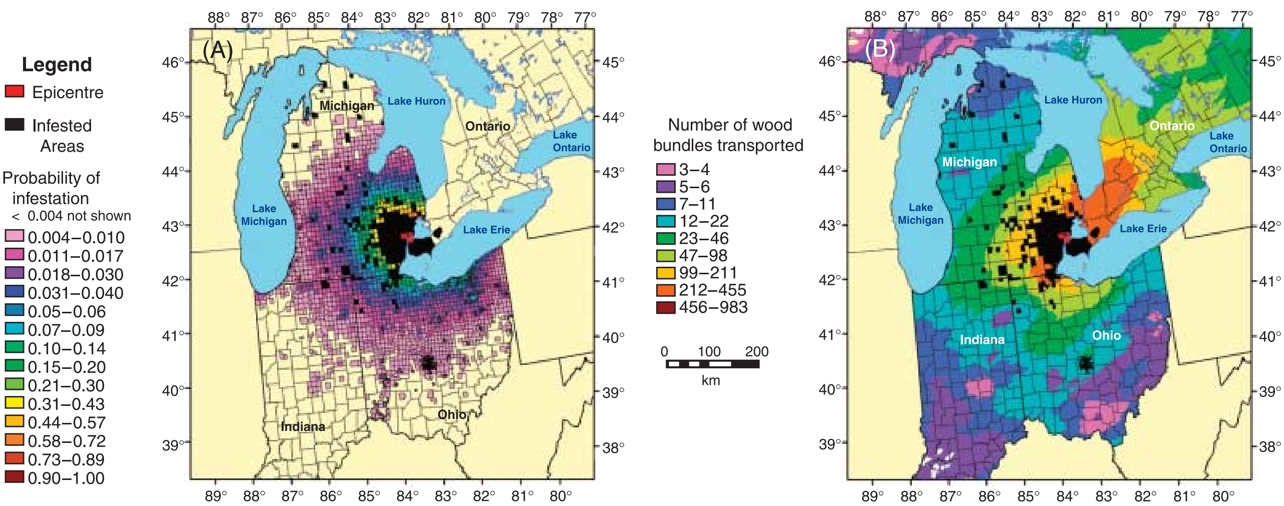


**Figure 2** Probability of invasion based on township/municipality population size and distance from the epicentre (a). Both population size and distance were log-transformed. Also shown are areas at risk of infestation in Michigan, Ohio, Indiana and Ontario based on long-distance transport of firewood (b).

**Table 2** Cross-validation of the logistic regression model that incorporated both log-transformed human population size and log-transformed distance from epicentre to predict invasions by emerald ash borers in the three Great Lakes states (MI, OH, IN) based on 2004 data. $N = 867$ townships and municipalities

| Observed | Predicted invaded | Predicted non-invaded | Total | % correct |
|---|---|---|---|---|
| Invaded | 31 | 17 | 48 | 64.6 |
| Non-invaded | 5 | 814 | 819 | 99.4 |
| Total | 36 | 831 | 867 | 97.5 |

where $d$ is the log-transformed distance (km) and $n$ is the log-transformed population size. This model correctly classified 64.6% of the invaded sites and 97.5% of all sites overall with regard to their invasion status based on these two parameters (Table 2). Distance from the epicentre was the most important determinant of this relationship, and thus invasion probabilities form concentric circles from Detroit (Fig. 2a). The ability of the model to correctly classify invaded sites declined with distance from the epicentre, and was poor with respect to invaded sites in the northern end of Michigan's lower peninsula. The only two sites correctly classified as invaded in these outlying areas were Greenbush and Oscoda townships (Alcona and Iosco counties) and Grand Traverse (Fig. 2a). The model suggests that the areas of Gary and Fort Wayne, Indiana, and Bay City, Michigan, are at moderate risk of invasion ($P = 0.01$–$0.04$), whereas risk is slightly lower in Indianapolis, Indiana, and Cincinnati and Dayton, Ohio (Fig. 2a).

A gravity model was developed to predict dispersal across spatial scales using information on the quantity of firewood transported between the epicentre of Windsor, Ontario and provincial parks in the province that were frequented by campers, the number of campsites at each park frequented, and distance between the epicentre and park (Fig. 2b). Although the model was developed for Ontario, we also applied it to Great Lakes states. Areas at highest risk of firewood-vectored dispersal form an ellipse bordered by the south-eastern edge of Lake Huron in Michigan and Ontario and the south-western edge of Lake Erie in Michigan and Ohio (Fig. 2b). The latter areas already support some borer populations, and are also highly vulnerable to diffusive dispersal, whereas vulnerable areas in Ontario lie well outside of the current quarantine zone, are distal to the firewall, and are currently borer-free.

## DISCUSSION

Introduced beetles are often associated with significant damage to forests, caused either directly through their boring or feeding activities or indirectly by serving as vectors for pathogen transmission (e.g. see Allen & Humble, 2002; Haack, 2003). A number of introduced boring beetles currently threaten North American forests, including the pine shoot beetle *Tomicus piniperda* in the greater Great Lakes region (Haack & Poland, 2002), the Asian longhorned beetle *Anoplophora glabripennis* in New York, Chicago and Toronto (e.g. Auclair *et al.*, 2005), and the brown spruce longhorn beetle *Tetropium fuscum* in Nova Scotia (Smith & Hurley, 2000). Emerald ash borers were discovered in the Great Lakes region during summer 2002, and pose an enormous threat to native ash forests in eastern North America. By 2004, ash mortality rate in infested areas in south-western Michigan was positively correlated with proximity to the epicentre of the invasion, and highest (61%) in Wayne County, the focal point of the invasion (Witter & Storer, 2004).

As with all invasions, an important determinant of invasion success is introduction effort (see Colautti *et al.*, 2006; Memmott *et al.*, 2005). It is imperative that we collect comprehensive data pertaining to the density and geographical distribution of imported propagules to predict identities of possible invaders and the locales where invasions may occur. This requirement is typically met by national screening programs that allow identification of species intercepted as they enter the country (see case studies in Ruiz & Carlton, 2003). Haack (2003) provided one such example for scolytid beetles entering ports in the USA, based on the Animal and Plant Health Inspection Service's (APHIS) inspection records.

Once non-indigenous species have established, additional models are needed to predict spread based on patterns and density of propagule dispersal. Models developed here address dispersal patterns of the emerald ash borer in North America by both local diffusion and long-distance transport. New reports of the beetle increased very rapidly between its first description in 2002 and 2005. A high proportion (77%) of invasions reported in 2004 conceivably resulted from diffusive spread ($P \geq 0.05$), although a much lower percentage (23%) of these can be ascribed to diffusion with higher certainty ($P \geq 0.76$; Fig. 1c; Table 1). Virtually all of the reports that could not be explained by diffusive spread occurred in the upper regions of the lower peninsula of Michigan, distal to the primary invasion front. All of the invasions reported thus far in 2005 are in areas with high probability of diffusive spread (Fig. 1d). Some of the new populations that cannot be accounted for via diffusive spread are consistent with the logistic regression model based on distance from the epicentre and on human population size in the recipient area (Fig. 2a). Nevertheless, even this model was unable to account for 17 of the 48 new populations in the Great Lakes states during 2004 (Table 2). Many of these populations were located in the same region of Michigan that could not be explained by diffusive spread. Some of these populations were found in areas where humans transport firewood, albeit at low frequency (Fig. 2b).

The logistic regression model had a greater error rate in predicting invaded sites as non-invaded (17 of 48 = 35%) than non-invaded sites as invaded (5 of 36 = 16%). This finding supports the concept that diffusive dispersal from the epicentre occurs with much greater predictability than long-distance dispersal to peripheral areas (Table 2). This pattern is also consistent with theoretical models that suggest predicting location of invasions in peripheral areas can be very difficult (e.g. Lewis, 1997). Nevertheless, knowledge of current distribution can be used to formulate risk assessment and management strategies. For example, 'trap' or sentinel trees are now used in the USA to detect and provide a semiquantitative measure of migrating emerald ash borers in areas where dispersal is anticipated. This approach has been used for other introduced pest species. For example, pheromone traps have been successfully deployed to detect early spread of the gypsy moth, *Lymantria dispar* in Michigan (Gage *et al.*, 1990).

An alternative to the vector-based approach is provided by ecological niche modelling, in which a non-indigenous species' ecological requirements are characterized for its native range and then applied to the landscape in the actual or potentially invaded region (e.g. Peterson, 2003; With, 2004). Peterson and Vieglais (2001) utilized this approach to determine the possible range of Asian longhorned beetles in North America. Ecological niche modelling allows identification of areas vulnerable to establishment of the non-indigenous species, with the implicit assumption that propagules are available to transport the species to these locations. The most promising possibility to predict future ranges of non-indigenous species is to marry vector-based and ecological niche modelling approaches. This methodology would allow identification of vulnerable sites based on vector and pathway studies, following which the model could be refined based on the match between the species' ecological needs and the habitat's characteristics. A simple application of this approach was provided by Peterson (2003), who noted that although areas in California should be vulnerable to Asian longhorned beetles — based on shipping traffic inbound from Asian source ports — available habitats in most port areas would be inhospitable to the beetle's needs. MacLeod *et al.* (2002) concluded that Asian longhorned beetles pose a significant threat of establishment, spread and economic damage in southern Europe based on a CLIMEX niche model. A CLIMEX model that incorporated both temperature and moisture was used to evaluate possible establishment and spread of the red imported fire ant *Solenopsis invicta* in New Zealand and Australia (Sutherst & Maywald, 2005). Before similar niche modelling can be applied to the emerald ash borer across North America, information must be obtained on key aspects of its biology, including its thermal limits in Asia. Nevertheless, approximately 9 billion ash trees inhabit and are potentially at risk in the USA and Ontario (Nowak, 2003; K. Marchant, unpublished data). As the beetle is already present in areas with large numbers of vulnerable hosts in the Great Lakes region, this area remains highly susceptible to additional spread and harm.

Our models are based on observed ash borer distributions between 2002 and 2005, and surveys of campers entering provincial parks in Ontario. A number of uncertainties are implicit to our models. First, our diffusion model is based on changes in reported distribution between 2002 and 2003, and assumes that diffusion rate is invariant over time. Second, because of the threat posed by this beetle, manpower devoted to its study and control has increased through time, decreasing the likelihood of missing established populations (reduced type II error). This could be particularly important for populations distal to the epicentre, which may have been underreported in earlier years. If so, our diffusion model would underestimate early and overestimate later spread. Third, current eradication efforts, especially in outlying 'nascent foci' (Moody & Mack, 1988), could dramatically reduce the size of borer populations available to disperse to adjacent areas. These suppression efforts could effectively lower the probability of dispersal and increase the area less vulnerable to diffusive spread (Fig. 1c,d). Fourth, our firewood model was developed using data for parks in Ontario, but applied to both Ontario and the Great Lakes states, assuming that behaviour of campers is similar in both countries. Differential success of public education campaigns — including the deployment of quarantine notification signs on major highways — between the USA and Canada, would affect spatial patterns of firewood transport and thus the vulnerability of long-range dispersal. At present, we are unable to test this possibility. Finally, there are a number of sites that have been invaded that cannot be accounted for by any known vectors. It is possible that other unidentified vectors may transport beetles to these sites, or that predictor variables may have been incorrectly parameterized. For example, both distance from the epicentre and human population size of the recipient area were $\log_e$-transformed in the logistic regression model. It is possible that some outlying areas that were expected to have very low visitation rates of individuals arriving from the epicentre may, in fact, have had a much higher rate owing to site attractiveness or some other measure not considered in our model. This would create a 'fat-tail' in the dispersal kernel of human vectors (Lewis, 1997), and increase the probability of invasion at greater distances. For example, one of the outlying areas invaded in our study was near Traverse City, Michigan, which is a very popular tourist destination for individuals from metropolitan Detroit.

Quarantine efforts may be willfully disregarded by some members of the public. For example, illegal transportation of infected ash saplings was responsible for the introduction of emerald ash borers to Maryland. During 2004, four new sites were discovered infested in Maryland. The rapid implementation of eradication procedures in that state following these discoveries, combined with intensive follow-up surveys, indicates that borer has been controlled and possibly extirpated from the region. Only a single larva was found at each of four sites of outplanted trees during 2004 (Fig. 2a). Likewise, no new invasions have been reported in Virginia following implementation of quarantine measures there. Intensive surveys should be repeated in future years in both states to confirm that the species has in fact been extirpated.

Quarantine in Michigan and Ontario is a far more arduous task than in Maryland and Virginia, as new infestations could result from many different source populations. Most new reports of borer invasions in Michigan during 2004 occurred outside of the quarantine zone, and all of the sites reported thus far in 2005 have been outside but contiguous to quarantine zones. Unless local dispersal from these currently isolated colonies can be curtailed, infilling of the distribution may be expected (Fig. 1d). The 23 infestations reported in Ontario during 2004 (Fig. 1c) were located in close proximity to one another, and all were outside the eastern boundary of the ash-free zone. Moody and Mack (1988) stressed the importance of focusing on satellite populations in controlling spread of invading plants. Taylor and Hastings (2004) also suggested eradication prioritization for isolated, low-density *Spartina* colonies as opposed to high-density core populations owing to faster spread capabilities of the former.

Sharov (2004) explored the different treatment options available and the conditions under which each would be the optimal management strategy for a harmful, introduced species. He showed that the optimal strategy changes from 'eradication' to 'slow-the-spread' and then to 'do-nothing' as the distribution of the target species increases. In this context, the eradication programs in Maryland and Virginia seem appropriate, as does the 'control-the-spread' program using the ash-free zone in Ontario. Furthermore, local eradication programs directed toward satellite colonies in each of the political jurisdictions surrounding the Great Lakes can also reduce spread of the emerald ash borer. A 'slow-the-spread' management strategy that targeted isolated satellite colonies along the invasion front dramatically reduced the overall rate of spread of the gypsy moth in North America (Sharov *et al.*, 2002).

In summary, the emerald ash borer is a very destructive species that has colonized North America and is spreading quickly. The beetle is currently spreading via stratified diffusion through a number of natural and human-mediated mechanisms. Management based on the eradication of isolated colonies in Maryland and Virginia appears to have been successful, whereas range expansion in the Great Lakes region has continued despite deployment of an array of management strategies.

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