Predicting Argentine ant spread over the heterogeneous landscape using a spatially explicit stochastic model

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Abstract. The characteristics of spread for an invasive species should influence how environmental authorities or government agencies respond to an initial incursion. High-resolution predictions of how, where, and the speed at which a newly established invasive population will spread across the surrounding heterogeneous landscape can greatly assist appropriate and timely risk assessments and control decisions.

The Argentine ant (Linepithema humile) is a worldwide invasive species that was inadvertently introduced to New Zealand in 1990. In this study, a spatially explicit stochastic simulation model of species dispersal, integrated with a geographic information system, was used to recreate the historical spread of L. humile in New Zealand. High-resolution probabilistic maps simulating local and human-assisted spread across large geographic regions were used to predict dispersal rates and pinpoint at-risk areas. The spatially explicit simulation model was compared with a uniform radial spread model with respect to predicting the observed spread of the Argentine ant. The uniform spread model was more effective predicting the observed populations early in the invasion process, but the simulation model was more successful later in the simulation. Comparison between the models highlighted that different search strategies may be needed at different stages in an invasion to optimize detection and indicates the influence that landscape suitability can have on the long-term spread of an invasive species.

The modeling and predictive mapping methodology used can improve efforts to predict and evaluate species spread, not only in invasion biology, but also in conservation biology, diversity studies, and climate change studies.

Key words: Argentine ant; heterogeneous landscape; invasive species; Linepithema humile; long-distance dispersal; New Zealand; pest risk assessment; spatially explicit model; spread rate.

INTRODUCTION

Increase in world tourism and trade has been linked to a rise in the number of species unintentionally introduced to new environments (Levine and D’Antonio 2003). The establishment of a new species in an area where it is not normally found is often associated with severe ecological and economic consequences (Mack et al. 2000, Pimentel et al. 2000). If that species is determined to have the potential to spread over a large area and have a negative impact, then eradication or control actions must be quickly prioritized to minimize damage.

Once an exotic species establishes a reproducing population in a new region, the next stage of the invasion process is its spread across the landscape (Hastings 1996). A model that can estimate the rate of spread and the direction of an invasion would greatly assist relevant authorities in the design of sampling programs for detection and in the monitoring of spread and eradication attempts. However, modeling spread is difficult for two reasons. First, data for model parameterization are not usually available to estimate the rate of spread of a newly detected species. Second, many species can spread by multiple methods, for example, by natural means, often a diffusion-like process, and also by large jumps, often mediated by humans, a process often referred to as stratified diffusion (Hengeveld 1989).

If such components are characteristic of a new invader, strategies for slowing its spread must account for the effect of each component on both temporal and spatial aspects of dispersal.

Previous methods for modeling spread have provided theoretical insights into the potential speed at which a population front might travel and have highlighted important factors that impact the rate of spread (for an extensive review see Hastings et al. [2005]). Those factors include dispersal kernel shapes that describe the distance that propagules travel and Allee effects that can limit spread rates and constrain population fronts that otherwise are predicted to accelerate indefinitely. To date, most models focus on an abstract environment that is typically homogenous and constrained to one dimen-
sion (e.g., Kot et al. 1996) or if not, they are constrained with respect to scale. More realistic models are needed to progress practical understanding of the dispersal and spread of organisms and to provide decision support for those involved with containing or eradicating invasive species. Moreover, a model using an incorrect spatial dimension can produce misleading results. A good example is a study by Petrovskii (2005) in which it was shown that the invasion of a predator or infectious disease that has a patchy spatial distribution can persist in two-dimensional space, but will go extinct in a corresponding one-dimensional system. Of critical importance also is that an abstract, one-dimensional model excludes spatial patterning that arises from the interaction of a population with the landscape. Turner et al. (1993) were among the first to suggest that an essential component to the progress of predictive spread models is to utilize the spatial heterogeneity of the natural landscape, and Worner (1994) called for models of species establishment and distribution to be integrated with geographic information system (GIS) technology.

In this study we incorporate realistic landscapes into a spread model by modeling dispersal processes within a GIS. The model uses concepts taken from traditional theoretical population and spread models and applies them to the simulation of the dispersal of the Argentine ant (Linepithema humile, Mayr) in New Zealand.

The Argentine ant, Linepithema humile, is a worldwide pest that is cited as one of the six worst invasive ant species (Holway et al. 2002). When this species was first recorded in New Zealand in 1990 (Green 1990), there was no attempt to control it as it was considered already well established. Argentine ants are considered a successful “tramp” ant species (Passera 1994) in part due to a strong tendency to move and associate with humans (Suarez et al. 2001), its unicoloniality (individuals mix freely among physically separate colonies) (Holway 1998), strong interspecific aggression (Holway 1999), polygyny (Keller and Passera 1990), and dispersal by budding (a queen supported by as few as 10 workers can establish a new colony) (Hee et al. 2000).

Linepithema humile is a threat to New Zealand’s biodiversity because in addition to potential negative impacts on wildlife, it readily displaces other ant species (reviewed in Holway et al. 2002). The displacement of existing ant species can cause complex mutualisms to be disrupted (Bond and Slingsby 1984, Lach 2003) as well as disrupt other ecosystem processes (Harris 2002).

Because L. humile was considered well established and there were limited means to control it, the species was largely left to spread unhindered and provides a good example to study the spread of an invasive species that is not confounded by an eradication attempt. International data on L. humile distribution and spread were used to parameterize a model that was then used to simulate L. humile spread from its initial site of invasion in New Zealand. While the distances of jump dispersal events and their frequency in New Zealand were used for comparison with international data, the exact spatial locations from New Zealand occurrence data were kept for model validation.

**Methodology**

**Model design**

A modular dispersal framework was used to model temporally discrete dispersal processes within GIS. Raster maps were used to represent population distributions and the modeling framework utilized open-source software and was implemented using the programming languages Python (available online) and C, within the open-source GIS GRASS (Neteler and Mitasova 2004). The L. humile model uses a raster map for each year to represent either the presence or absence of the species in a raster cell. The modular framework was designed as a generic simulation model that could be used for any species.

In this study, the dispersal of L. humile is characterized by stratified diffusion (Shigesada et al. 1995) with the invasion proceeding from several locations or foci. Such patchy distributions are often the result of the interaction of more than one mode of dispersal and Barber (1916), Holway (1995), and Suarez et al. (2001) indicate the two most influential dispersal modes for L. humile are local spread by budding and jump dispersal facilitated by human transport. Providentially, splitting the dispersal process into two components addresses the frequent problem of finding an appropriate dispersal kernel to represent dispersal distances. In our model, the two dispersal modes are represented in the model by local and kernel modules, respectively (Fig. 1a, b).

For any time step, the local module processes a raster map comprised of cells. For each occupied raster cell (in which the species is present), the model updates neighboring cells such that each becomes occupied, leading to contiguous spread of the population. Linepithema humile has been shown to have an average budding spread rate of 150 m/yr for regions where habitat and climate are not limiting (Suarez et al. 2001). To represent this spread rate at the correct resolution, the model used a raster resolution of 150 m and the local module used a von Neumann neighborhood to represent local dispersal (Fig. 1a).

The kernel module represents jump and long-distance dispersal and is based on the Cauchy probability distribution to represent the probability a dispersal event travels a given distance (Hastings et al. 2005). For each occupied raster cell, the kernel module first samples a Poisson distribution, with mean λ, to determine the number of long-distance dispersal events that arise from that cell. Then, for each of these events, the module samples the Cauchy probability distribution for the dispersal distance of each event. After the distance of the dispersal event is determined, the model samples a

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4 (http://www.python.org/)
uniform distribution in the range \([0, 2\pi]\) to establish the angle or direction of that event.

Habitat suitability and survival

To link the dispersal model to the real landscape where habitat suitability is variable, another module, survival, controls the probability an occupied cell becomes extinct. The probability of extinction is based on a suitability map that indicates the relative suitability of cells within the region being studied. The suitability map could potentially be constructed using any number of methods for modeling potential distributions of species based on environmental conditions (e.g., Worner 1988, Stockwell 1999, Sutherst et al. 1999, Thuiller 2003, Guisan and Thuiller 2005, Gevrey and Worner 2006, Pitt et al. 2007). For *L. humile*, however, we combined expert knowledge about the suitability of various land cover types for persistence of populations of this species (Harris 2002) with a degree-day analysis that measures the cumulative amount of heat required for continued development at any location (Hartley and Lester 2003).

For land cover, the New Zealand Land Cover Database version 2 was used (available online). Land cover types were divided into three categories, from unsuitable to highly suitable (H0, H1, H2), with a separate category for urban areas (HU). A category for urban areas was used because *L. humile* has been found to survive at lower ambient temperatures in urban environments, because of a close association with human activity and the warm microclimates created by that activity (Suarez et al. 2001). The land cover suitability map is shown in Fig. 2a. Thirty years of historical daily minimum and maximum temperatures interpolated as a grid with a latitudinal and longitudinal resolution of 0.05° were used to create a map of the annual average degree-days for *L. humile* development above a threshold of 15.9°C (Hartley and Lester 2003). This map was transformed to the New Zealand Map Grid (NZMG) projection and interpolated, using inverse distance squared weighting, to a resolution of 150 m. Based on the degree-days required for development, the degree-day map was divided into four categories of total degree-days from low to high suitability (T0 < 200, T1 = 201–300, T2 = 301–400, T4 > 401 degree-days) (Fig. 2b).

The land cover and degree-day suitability maps (Fig. 2a, b) were combined (Fig. 2c) using the scheme presented by Harris (2002) as shown in Table 1. Harris (2002) used mean annual temperature classified into suitability levels, whereas in this study, degree-days have been substituted, because they are biologically more relevant and usually more accurate. The result was a map classified into regions of low, medium, and high suitability, with additional categories for regions with unsuitable land cover or that were too cold. Each category was assigned a survival probability indicating the probability of occupants surviving to the subsequent year, with progressively lower probabilities for less suitable categories (Table 1).

The overall suitability map (Fig. 2c) was constrained predominantly by the degree-day map, which resulted in most of the central and southern parts of the North Island classified as too cool for *L. humile* development. Much of Northland, along with Auckland and other northern cities and towns, showed medium or high suitability. Northeastern and some eastern coasts showed low suitability.

Model calibration

To calibrate the kernel module, data from the historical spread of *L. humile* in the United States was used (Suarez et al. 2001). The data included average rates of spread as a consequence of the budding process across multiple invasion fronts as well as the dates of first detection within U.S. counties from 1891 to 1999. Nearest-neighbor distances among established populations were used to fit the (Cauchy) probability distribution used in the kernel module to represent the frequency distribution of long-distance dispersal events. The nearest-neighbor distances were calculated each year as the distance between the centroids of new counties.

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**Fig. 1.** The three modules represented in the *Linepithema humile* (Argentine ant) dispersal simulation: (a) local dispersal to neighboring sites, using a von Neumann neighborhood to represent the dispersal ability of the ant; (b) long-distance dispersal; and (c) stochastic survival associated with occupied cells based on an underlying suitability map.
invaded by *L. humile* and the centroids of counties that had previous records of presence. For counties that were noncontiguous, the average of the region centroids, weighted by area, was used. The number of new occurrences each year, divided by the number of preexisting occurrences, was used to estimate $\lambda$, the frequency of long-distance dispersal events as described by the Poisson distribution. Because of the scale over which the data were measured (over individual counties), the estimate of $\lambda$ that represents the number of new foci per year was likely to be a conservative underestimate. However, any underestimation of $\lambda$ would be offset in this model by local spread represented in the model by the local module that generates new sites neighboring those that already exist.

The frequency and distance of long-distance dispersal events are often difficult to quantify (Higgins and Richardson 1999), but good estimates are essential for accurate model construction (Shigesada and Kawasaki 1997). Despite the fact that the New Zealand *L. humile* occurrence data is point-based, compared with the U.S. data, which was recorded over geographic regions, the frequency of long-distance dispersal events and the frequency of dispersal distances could still be calculated. Sites that were within 300 m/yr of any of their neighbors were assumed to have established by budding and were ignored as per Ward et al. (2005), who previously had investigated the statistics of *L. humile* human-assisted dispersal distances in New Zealand.

Frequencies of *L. humile*’s long-distance dispersal events within the United States and New Zealand were examined to determine whether they occurred at similar scales. A qualitative assessment of dispersal events showed that, for both New Zealand and the United States, the majority of dispersal events occurred over relatively short distances, and the distribution in each country included several large-distance movements (Fig. 3). The U.S. data had a higher proportion of dispersal distances distributed between 100 and 700 km. These large dispersal distances were probably the result of two factors. First, North America is part of a large continent, so large human-assisted dispersal distances are possible, compared with New Zealand, which is a small island nation. Second, for the U.S. data, distances might be overestimated because of the size and shape of the counties on which they were based. For example, a dispersal event may cross the short distance from one side of a border between two counties, but the distance...

**Table 1.** Scheme used for combining land cover and degree-day suitability maps.

<table>
<thead>
<tr>
<th>Combination</th>
<th>Result</th>
<th>Survival probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>T3 + H2, T3 + HU, T2 + HU</td>
<td>high suitability</td>
<td>100</td>
</tr>
<tr>
<td>T3 + H1</td>
<td>moderate suitability</td>
<td>80</td>
</tr>
<tr>
<td>T1 + HU, T1 + H1, T2 + H1, T1 + H2, T2 + H2</td>
<td>low suitability</td>
<td>50</td>
</tr>
<tr>
<td>H0 + T*</td>
<td>unsuitable habitat</td>
<td>10</td>
</tr>
<tr>
<td>H* + T0</td>
<td>too cold</td>
<td>10</td>
</tr>
</tbody>
</table>

**Notes:** Land cover types were divided into three categories, from unsuitable to highly suitable (H0, H1, H2), with a separate category for urban areas (HU). Based on the degree-days required for development, the degree-day map was divided into four categories of total degree-days from low to high suitability ($T0 < 200$, $T1 = 201–300$, $T2 = 301–400$, $T4 > 401$).
recorded will be the larger distance between the centroids of the two county regions.

We used the U.S. frequencies for parameter estimation of the Cauchy distribution. The Cauchy distribution was chosen to represent the distances of dispersal events as it is "fat-tailed," allowing for rare events at extreme distances that have been shown to be an important characteristic of the dispersal of many species (Hengeveld 1989, Higgins and Richardson 1999, Clark et al. 2001, Suarez et al. 2001) and even that of humans (Brockmann et al. 2006). Maximum likelihood estimation (MLE) using the simplex search method was used (Lagarias et al. 1998) to estimate the Poisson $\lambda$ and the Cauchy $\gamma$. Maximum likelihood estimation estimated $\gamma$, the shape parameter for the Cauchy distribution, as 8.37 $\times$ 10^4 (Table 2).

A comparison of the frequency of dispersal events per site for each country showed a greater frequency of a low number of dispersal events per site in the United States, although both countries showed averages per site less than 1 (Fig. 4). The greater frequency of low numbers of dispersal events per site in the United States is best explained by the longer time frame over which dispersal was recorded. Also, as the species became established in more counties it became harder for dispersing ants to find unoccupied counties in which to establish. Maximum likelihood estimation estimated $\lambda$ for the Poisson distribution that represents the frequency of dispersal events as 0.298 (Table 2).

**Simulation**

For this study, the simulation was constrained to the North Island of New Zealand, an area of 113,729 km², at a raster resolution of 150 m. Within the GIS, the simulation was carried out on the 1949 New Zealand Geodetic Datum and the NZMG projection. The time step was one year, and within each time step the *Linepithema humile* distribution map was processed by the model modules in the order: local, kernel, and survival. At the end of each time step the distribution map is saved for later analysis. The simulation was run from 1990 to 2005, starting with the three sites discovered in 1990.

To measure the uncertainty of prediction to variation in model parameter values, the parameters for the Poisson mean $\lambda$ and the scale parameter, $\gamma$, of the Cauchy distribution were simulated over their estimated mean value and their 95% confidence interval (CI) limits, for a total of nine combinations of parameter values. Both the kernel and survival modules involve random sampling from appropriate probability distributions and are therefore stochastic processes. Thus, each parameter combination was simulated 100 times from 1990 to 2005 to give 900 realizations of spread.

To obtain an average representation of *L. humile* spread, all maps for a given year were averaged to create an occupancy map that represents the probability a cell is occupied at a given time. This probability is simply the proportion of times a cell was occupied over the 100 simulations. This occupancy map was then masked by excluding areas below a given threshold or a very low probability of occupancy.

To evaluate the performance of the *L. humile* simulation model against a simple spread model, uniform radial spread from the mean center of the three initial invasion sites was also modeled. A linear increase

**Table 2.** Maximum likelihood estimation (MLE)-derived parameters for the probability distributions used for simulating long-distance human-mediated dispersal events with the kernel module.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>95% lower bound</th>
<th>Estimate</th>
<th>95% upper bound</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cauchy $\gamma$</td>
<td>72,700</td>
<td>83,700</td>
<td>94,600</td>
</tr>
<tr>
<td>Poisson $\lambda$</td>
<td>0.199</td>
<td>0.298</td>
<td>0.428</td>
</tr>
</tbody>
</table>
in the square root of area is equivalent to a constant spread rate for a circular area. The rate of radial increase for the uniform spread model was calculated by assuming the square root of the increase in area of the simulation model over time was approximately linear and by calculating an approximate slope. The rate of increase of the uniform spread model radius was given by

$$\sqrt{A_{t}} = \sqrt{A_{0}} \frac{t - t_0}{t_1 - t_0}$$

where $A_t$ is the area encompassed by the simulation model at time $t$, and $t_1$ is some time after $t_0$. This formula meant that both models encompassed approximately the same total area at any time step. Simulation results indicated that certain phases in the increase in occupancy area had the square root of their area increase at an approximately linear rate.

**RESULTS**

The percentage of observed *L. humile* occurrence sites in New Zealand for each respective year that fell within the occupancy envelope was calculated (Fig. 5a). The model at all occupancy thresholds predicted a high percentage of sites early in the simulation, before dropping to ~40% of observed sites at 1993–1994. The percentage of observed sites predicted by the model (occupancy threshold > 0) increased in 1996. The percentage of predicted sites at >5% and 10% occupancy follow, both peaking in ca. 1999. The percentage of

![Graph](image)

**Fig. 4.** Comparison of long-distance dispersal event frequency for *Linepithema humile* (Argentine ant) per number of preexisting sites in New Zealand and the United States.

![Graph](image)

**Fig. 5.** Performance of the simulation model ($\lambda$ [the frequency of new dispersal events] = 0.298, $\gamma$ [the scale parameter of the Cauchy distribution representing dispersal distances] = 83700) with respect to the extent that the probability envelope includes observed *Linepithema humile* (Argentine ant) occurrence sites in a given year, 1990–2005. (a) The percentage of sites included. (b) The difference in performance (percentage of sites predicted) between the simulation model (number of sites within the probability envelope) and the uniform spread model (number of sites within the uniform radial spread). When the change in percentage is positive the simulation model performs better than the uniform spread model and vice versa when the change is negative.
Hotspots, or those areas with high values in the occupancy envelope, are of particular interest to agencies charged with eradicating or monitoring invasive species. In this study, hotspots included regions near the invasion epicenter, within and near Auckland city and nearby cities such as Whangarei and Hamilton, both of which have *L. humile* infestations. Towns near Auckland, such as Pukekohe and Waitakuru, were also indicated as hotspots, but to date have no recorded occurrences. Great Barrier Island, Little Barrier Island, Ponui Island, and Tiri Matangi Island were also indicated as hotspots. Great Barrier Island and Tiri Matangi Island have had occurrences reported, most likely from human-assisted dispersal. Both islands have undergone poison baiting treatments to eradicate *L. humile* (J. Boow, personal communication; C. Green, personal communication). The model indicated one large hotspot covering most of the Hauraki Plains, which has no recorded occurrences of *L. humile*. The land cover map indicates a large area of scrubland that is a highly suitable habitat for *L. humile* (Suarez et al. 1998). The whole of the Hauraki Plains also has a sufficient number of degree-days for complete *L. humile* development.

No simulation for any combination of variables reached the southern end of the North Island, despite that *L. humile* has been established there since 2000. This model result is probably due to the large area of unsuitable habitat between the invasion epicenter and the south of the North Island. The occurrences much further south likely arose from individuals hitch-hiking on road or rail networks. Over the entire simulation area (Fig. 8), high-suitability regions were more quickly occupied than low-suitability regions, as expected. Some low-suitability regions eventually did show significant occupancy probabilities despite the high probability of extinction through their proximity to high-suitability regions that provided high propagule pressure.

While there were differences in model output in response to variation in its parameters, the result after some time had elapsed was a qualitative pattern similar to the underlying landscape suitability map. This result reinforces the observation that landscape heterogeneity can often have a large stabilizing effect on ecological models (Kuno 1981, Ruxton and Rohani 1999, Gardner and Gustafson 2004). The simulation was most affected by differences in \( \lambda \), as that parameter controlled the number of events, with a cumulative effect so that more events earlier in the simulation led to more occupied sites from which successive events could occur.

Fig. 6 shows how the square root of area (\( \sqrt{A} \)) of the occupancy envelope increased through time. The rate that \( \sqrt{A} \) increased for all occupied sites with no occupancy threshold accelerated until 2000–2002 before the rate slowed slightly. The graphs for various occupancy thresholds seem to show approximately three phases with different rates of increase. The different rates seem to be due to the shape of the initial invasion area being an isthmus between the main land mass of the

![Figure 6](image-url)
North Island and Northland, with less area to spread than inland areas. However, once the invasion has spread far enough, it can reach these inland regions containing more area available for occupation.

**DISCUSSION**

Lonsdale (1999) suggests that more robust relationships in the pattern of invasive species spread are likely to emerge at broad spatial scales. Clearly, simulating the spread of a species over large spatial scales, such as in this study, is important to help progress theory concerning the dispersal and spread of organisms over the heterogeneous environment. We showed that it is possible to estimate how and where an invasive species might spread over a large spatial scale, by calibrating a stochastic and spatially explicit presence/absence model to observed data and combining that with expert knowledge.

When simulation results were compared using a uniform circular spread model with a constant radial
spread rate from the invasion epicenter, the uniform spread model was more accurate early in the invasion. The simulation model, however, predicted the observed long-distance events much more quickly as the invasion proceeded. The most demanding and costly aspect of monitoring, controlling, or eradicating an invasive species is the extent of the area to be searched. Clearly the ability to quickly identify hotspots for searching far from the perceived epicenter of an invasion would be very useful. In the case of *L. humile*, the simulation model matched the actual occurrence data for five hotspots (Auckland, Hamilton, Whangerei, Great Barrier Island, and Tiri Matangi Island) and has indicated that several other towns and the Hauraki Plains could potentially harbor populations of the ant, despite the fact that none have yet been reported in these regions.

The simulations in this study underestimated the rate of spread of the Argentine ant in New Zealand; no simulation reached the southern end of the North Island where the species has been established since 2000. Models often underestimate the rate of spread of invading organisms, and this failure is attributed to the inability to accurately measure infrequent long-distance dispersal (Andow et al. 1990, Liebhold et al. 1992, Buchan and Padilla 1999, Neubert and Caswell 2000). Despite this result, this study clearly highlights the importance of including long-distance dispersal when it has been shown to occur, since without it, species spread would progress much more slowly. Indeed, within the time frame of the simulation, 1990 to 2005, *L. humile* spread due to population diffusion (via budding) would not have spread beyond 2 km from each of the three initial occurrence sites. Even theoretical models such as integro-difference equation models of spread show that the long-distance component of dispersal ultimately decides invasion speed, even when long-distance dispersal is rare (Kot et al. 1996, Lewis 1997, Neubert and Caswell 2000).

In this study we noted that maps from early simulations using our spatially explicit stochastic simulation model had little agreement. That is an expected result however, as it is difficult to predict what will happen very early in an invasion because of the inherent randomness of the process, especially with respect to long-distance dispersal (Higgins and Richardson 1999). On the other hand, as the invasion progresses, the simulation occupancy envelope tends to conform to the underlying suitability map, suggesting that perhaps only a suitability map is required. However, the ability to estimate the rate at which the invasion occupies suitable regions gives authorities, charged with the task of monitoring or eradicating an exotic species, critical dynamic information that is superior to just an estimate of potential distribution such as that provided by current distribution models. The latter, however, are useful for pre-border pest risk assessment, as they can be used to indicate the initial site at which an exotic species might establish, given a pathway of arrival into the country. However, this simulation model could be used to explore invasions from a number of potential disembarkation points over a wide region. Mooij and DeAngelis (2003) suggest that because spatially explicit dispersal models utilize landscape details, they suffer less from uncertainty than simpler models. Despite the
variability of output of the simulation model in response to parameter change, output maps were qualitatively similar and in fact decision makers are likely to be interested in the relative probability of occupancy between regions that indicate those most at risk rather than the absolute occupancy value.

Situations in which the model presented here would be a poor choice include where established populations are confined to distinct and explicit patches of suitable habitat, such that all other areas outside of these patches is unsuitable. In such a situation, a metapopulation model (Hanski et al. 2000) or a stochastic patch occupancy model (Moilanen 2004) would be more appropriate. Another case is when a species spreads through a monocultural environment, such as in certain agricultural systems. Here the assumption of a homogeneous environment is appropriate and mathematical models such as partial differential equations (PDEs) and integro-difference equations (IDEs) would have benefits not available to a simulation over a complex landscape.

This model is capable of generating realistic realizations of spread that can be used to design appropriate, balanced sampling programs to detect or monitor an invasive species especially at low densities. Designs with different sample sizes and spatial and temporal patterns can be tested over a realistic landscape. Similarly, experiments using different eradication treatments, particularly investigating the pattern in which they are applied, can be carried out. Such experiments are rarely possible in reality. Moody and Mack (1988) point out that for species spreading by stratified dispersal, decisions whether to control small, distant foci or the main source population can greatly affect the impact and cost of control. A modular model means modifications, such as linking human-mediated dispersal to transport networks, wind dispersal of airborne life stages, local population growth, or cellular-automata-based rules, are easily implemented. The modular nature also forces consideration of the various behaviors underlying the patterns observed in species spread (Pitt 2008). Elucidating the underlying mechanisms driving such patterns makes models less arbitrary and links them to explicit spatial scales (Grimm et al. 1996).

In conclusion, stochastic, spatially explicit dispersal models integrated with GIS are required to incorporate ecological theory about dispersal with heterogeneous landscapes. Not only will they help progress our understanding concerning species spread, they allow predictions to be made about the direction and rate of the spread. The predictions not only inform invasion biology, they provide essential information that can assist the prevention of further spread by an invasive population or for efficient eradication attempts. Such models will also assist climate change studies by simulating the movement of species into new areas that become climatically suitable. Lastly, while maps are very useful communication tools, allowing model results to be easily conveyed to policy and decision makers, representing uncertainty is a problem. Stochastic simulations, as have been used in this study, provide probabilistic estimates that encapsulate some of the uncertainty involved in the prediction of invasive spread.

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