Modeling the spread of the Argentine ant into natural areas: Habitat suitability and spread from neighboring sites

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ABSTRACT

To predict a fine-scale invasion of Argentine ants (*Linepithema humile*) into a natural area from the surrounding suburban matrix, we introduce a grid-based invasion model, similar to a cellular automaton model. Our model was based on observations of ant presence and absence but, unlike other models based on presence–absence data, it incorporated the process of invasion by spread from neighboring areas. Simulations were parameterized from a statistical analysis of a 17-year survey of ant distributions in the Jasper Ridge Biological Preserve in northern California. We simulated the effects of Argentine ant presence at neighboring grid squares, distance to development, presence of the native winter ant *Prenolepis imparis*, and other habitat and climate variables, and used these models to simulate invasion over many decades. The best predictions of the extent of Argentine ant invasion were based on the distance of each site to developed areas. Adding the effect of neighbors improved the predictions of the time at which sites would be invaded. Winter ants responded mainly to vegetation cover. Our results suggest that Argentine ants may reach their potential distribution in insular urban reserves rapidly, perhaps within 10 years, and that reserve size determines whether the reserve is likely to become fully invaded.

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1. Introduction

1.1. Invasion models

Biological invasions can damage both natural ecosystems and human economic activities. It is important for land managers to predict where and how quickly invasions will occur, and researchers have developed a wide variety of models to accomplish these goals. Many invasion models fall into one of two categories: habitat suitability and mechanistic, which differ in application and in the data required to parameterize them (Jeschke and Strayer, 2008). Habitat suitability models can be parameterized using simple presence/absence data, but can predict only the outcome of an invasion, in eventual spatial extent, not the dynamic process leading to that outcome. By contrast, mechanistic models require detailed information to find values for the parameters, but can predict the course of invasions through space and time (Carrasco et al., 2010; Kot et al., 1996), and can be used to investigate the consequences of management interventions (Miller and Tenhumberg, 2010; Shea et al., 2010).

Habitat suitability models are used, when little information is available about an invasive species' population growth and dispersal, to identify regions similar to the invader's known range, where the invader would probably become established if it were introduced there (Jeschke and Strayer, 2008; Loo et al., 2007; Peterson et al., 2004). However, such species distribution modeling is predicated on the assumption that a species is in equilibrium with its environment. This may lead to an underestimate the extent of eventual invasion, because early in the invasion, when the invader may not yet have been introduced to all types of suitable habitat, equilibrium may not be reached (Jones et al., 2010; Robinson et al., 2010; Welk, 2004). Moreover, an invasive species may not prefer the same habitat in all parts of its range, due either to differences in biotic interactions or to physiological differences between populations (Dullinger et al., 2009; Rödder and Lötters, 2010; Sutherst and Maywald, 2005). Some models of habitat suitability avoid some of these pitfalls by basing their predictions on detailed measurements of physiological reactions to climate (e.g., temperature-dependent mortality or reproduction rates as in Abril et al., 2009; Hartley et al., 2006; Hartley and Lester, 2003), but this type of model requires detailed knowledge about the invader's physiology.

Mechanistic models, such as integro-difference models and individual-based simulations, predict the course of an invasion (Carrasco et al., 2010; Kot et al., 1996). They can be also be useful in identifying the best management interventions, e.g., by identifying which life stages have the greatest effect on population growth or

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spread (Shea et al., 2010). Their parameterization requires accurate and detailed information about population growth, dispersal and migration (Miller and Tenhumberg, 2010), and such data may be difficult to fit to a model (Münzbergová et al., 2010). Although rich in demographic detail, such models tend to overlook environmental heterogeneity or simplify it into suitable and unsuitable habitat (e.g., Guichón and Doncaster, 2008). Such simplification may be undesirable, for example if some sites are suitable for the invader in some seasons or years but not in others, leading to a fluctuating invasion front (Heller et al., 2006; Kuppinger et al., 2010; Sanders et al., 2001), or if the rate of invasion differs with habitat (Borgmann and Rodewald, 2005).

1.2. A model of Argentine ant invasion

Here we develop a model to predict the course of local invasions of the Argentine ant, *Linepithema humile*, that combines some of the features of both mechanistic and habitat suitability models. The model is parameterized using a previously published statistical analysis of an Argentine ant invasion within a northern California biological preserve (Fitzgerald and Gordon, 2012), which examined the effects of habitat, climate, and competition with a widespread North American dominant, the native winter ant, *Prenolepis imparis*. Our data consist of observations of Argentine ant presence and absence at fixed sites, made each year for 17 years at about 200 sites on a 100-m grid across the 481-ha Jasper Ridge Biological Preserve in northern California. By tracking invasion into and retreat from each site we examined changes in the distribution over time, and examine how a variety of factors influence the course and extent of the invasion. We included the effects of the native winter ant because it is one of the few native ant species that coexists with and even resists Argentine ant invasion (Fitzgerald and Gordon, 2012; Sorrells et al., 2011; Suarez et al., 1998). To reduce the negative effects of spatial autocorrelation (Bini et al., 2009), the analysis explicitly incorporated the effect of neighboring sites on invasion status, and incorporated random effects of site to account for similarity among nearby sites.

Like habitat suitability models, the simulation model we develop here is based not on detailed demographic measurements but on observations of Argentine ant presence and absence. The 17-year sequence of data makes it possible to predict, as in mechanistic models, how Argentine ant invasion will proceed over time. Our model also incorporates the effects of habitat features, such as distance to developed areas, which make it possible to consider how a preserve's design may influence the spread of the Argentine ant. Thus our model takes a statistical approach similar to that of some habitat suitability models, but incorporates the processes of invasion and retreat. The model we develop here builds on our previous statistical analysis to reproduce the movement of Argentine ants through the landscape, to extrapolate the invasion's spread in the future, and to predict invasive spread in several local natural preserves. By tracking invasive spread from year to year and from season to season, we identify which sites will become invaded and when the invasion will occur. We use the model to identify how habitat features influence Argentine ant invasion and retreat.

1.3. Previous studies of Argentine ant invasion

Argentine ants have been introduced around the world, and have become invasive in all major regions of Mediterranean climate (Suarez et al., 2001). Argentine ants, like many invasive species, are most commonly found in and around developed areas. In some places introduced populations of Argentine ants cannot survive winter outdoors, but require protection in buildings (e.g., Minnesota: Suarez et al., 2001). In other regions, Argentine ants

commonly inhabit urban and suburban areas, but occur in only a few types of natural habitats, or at the urban edges of preserves (e.g., in Southern California: Bolger, 2007; Holway and Suarez, 2006; Suarez et al., 1998). In such areas, larger tracts of preserved land may provide a refuge for native ant species (Suarez et al., 1998). Several studies predict Argentine ant invasions on a regional or global scale, either by extrapolation based on current distributions (Pitt et al., 2009; Roura-Pascual et al., 2004, 2009) or by finding regions that appear to satisfy their physiological temperature requirements (Abril et al., 2009; Hartley et al., 2006; Hartley and Lester, 2003). Some of these studies explicitly account for the Argentine ant's use of urban environments (e.g., Pitt et al., 2009); others do not (e.g., Hartley and Lester, 2003). On the scale of a few kilometers, however, we know of only one study that predicts the outcome of an Argentine ant invasion in a natural area (Hartley et al., 2010), and none that predict the course of an invasion from a developed area into a natural area.

Seasonal polydomy may influence the course of Argentine ant invasions. Argentine ant colonies consist of groups of shallow, often temporary nests connected by trails. Each colony is based around a relatively permanent cluster of nests, occupying about 250 m², into which the entire colony aggregates during winter (Heller and Gordon, 2006; Heller et al., 2008a). In the summer, some nests in the winter aggregation area remain in use, while the colony forms many smaller nests, linked by trails over a large area of about 650 m² (Heller et al., 2008a), that move frequently in response to microclimatic variation or food availability (Heller and Gordon, 2006). Argentine ant queens do not participate in mating flights, so new nests are founded when groups of workers and queens walk to the new nesting site (Ingram and Gordon, 2003; Suarez et al., 2001). The seasonal expansion and contraction of individual colonies is reflected at the local scale in the changing invasion front, which moves forward during the summer, but retreats or stays in the same place during the winter (Heller et al., 2006; Krushelnycky et al., 2004; Sanders et al., 2001). The invasion front may also retreat due to colony failure in sites near the invasion front, but to our knowledge no studies have explicitly connected colony failure to retreating Argentine ant invasion fronts.

2. Materials and methods

2.1. Data collection

2.1.1. Main survey location and procedure

Data were collected at Jasper Ridge Biological Preserve, a 481-ha preserve located in northern California at 37°24′29″N, 122°13′39″W. The preserve includes a variety of natural habitat types, surrounded by low-density suburban development. A few roads, buildings, and parking lots are located within the preserve.

Our work is based on 17 years of data from an ongoing survey of the Argentine invasion at Jasper Ridge (Fitzgerald and Gordon, 2012; Heller et al., 2006, 2008b; Human et al., 1998; Sanders et al., 2001). The preserve was surveyed for ants twice a year, once in May and once in September, between May 1993 and September 2009. Survey sites were arranged on a 100 m grid superimposed over the entire preserve. Some areas were never surveyed due to poison oak or difficult terrain. At each survey site, a circle with radius of 20 m was searched for 5 person-minutes, and the genus of all ants found was recorded. Between 1993 and 1996, at some sites ants were not identified to genus, and instead categorized as Argentine or native ants.

Argentine ants have been present in the local area since the early 20th century, and may have entered the preserve originally from the surrounding suburban development (Human et al., 1998). For the first several years of the study, between 1993 and 2000, the invasion expanded toward the interior of the preserve. Since 2001,

the invasion boundary has stalled, or even retreated. Seasonal fluctuations continue, but very few survey sites have been invaded for the first time, and Argentine ants have retreated from some sites.

2.1.2. Additional survey locations

During September and October 2008 and April 2009, additional ant surveys were conducted at nearby Fremont Older Open Space Preserve and Pulgas Ridge Open Space Preserve. These are recreational and conservation areas in northern California owned by the Midpeninsula Regional Open Space District, and are open to the public. Fremont Older is a 299-ha park located at 37°18′03″N, 122°04′05″W, surrounded by suburban housing development, agricultural land, a golf course, and a county park. Pulgas Ridge is a 148-ha park located at 37°28′40″N, 122°17′32″W, and is bordered on one side by an 8-lane highway, with associated off-ramps and a rest area, and on the other sides by suburban development. The ant surveys at Fremont Older and Pulgas Ridge followed the same protocol as the ant survey at Jasper Ridge. Sites on a 100-m grid were surveyed in all accessible areas of Pulgas Ridge and in the eastern portion of Fremont Older.

2.2. Statistical models of changes in ant distribution

Previous work showed that Argentine ant invasion and establishment were linked most strongly to proximity to developed areas and the proportion of neighboring survey sites with Argentine ants present (Fitzgerald and Gordon, 2012). Other factors, with significant effects that depended on season, were the presence of the native winter ant, *P. imparis*; features of the habitat such as vegetation cover, distance to water, and elevation; and variation in temperature and rainfall (Fitzgerald and Gordon, 2012; Appendix A). Dense tree or shrub cover was the variable most closely associated with an active winter ant presence. Argentine ant presence was associated with changes in winter ant activity more consistently than the reverse. Weather, distance to water, elevation, neighboring sites with winter ants, and distance to development also played roles in winter ant distribution, with effects that depended on season (Fitzgerald and Gordon, 2012, and see Appendix A).

2.3. Simulation models

2.3.1. Model description
2.3.1.1. *Starting conditions.* We simulated changes over time in Argentine ant and winter ant distribution, using a grid-based model we created in MATLAB. Each hectare of Jasper Ridge was represented as a square on a grid, with grid squares centered on ant survey sites. Using transition probabilities derived from the previous analysis of survey data (Fitzgerald and Gordon, 2012), we simulated the arrival and persistence of Argentine ants and winter ants in each grid square from 1994 to 2009. For grid squares corresponding to sites that were surveyed in 1994, the initial presence and absence of each species was based on the 1994 ant survey data. For all other grid squares where there were no corresponding data on Argentine and winter ant presence in 1994, we randomly assigned the initial distribution of presence and absence. To make the random assignment, for each of the grid squares for which there was no survey data, we assigned a probability equal to the proportion of the surveyed sites occupied by Argentine ants. We assigned initial winter ant presence in the same way, independent of initial Argentine ant presence.

2.3.1.2. *Seasonal transitions.* We simulated changes in ant distribution separately for three sets of seasonal transitions: (1) from fall to fall (1-year fall simulations) and (2) from spring to spring (1-year spring simulations); and (3) from spring to fall and back to spring (6-month simulations). The simulations were performed separately because seasonal nest movement in Argentine ants, with spread in the spring and contraction in the fall, contributes to the observed pattern of invasion. Each simulation covered a period of 15 years, either in 15 time steps each representing one year, for (1) and (2) or in 31 time steps each representing six months for (3).

2.3.1.3. *Simulations of Argentine ant distributions based on five sets of variables.* At each time step, each grid square was assigned a probability of Argentine ant presence at the next time step (see Appendix A). We ran separate simulations in which the probability of arrival and persistence depended on five different subsets of the variables (Table 1 and Appendix A). First, we tested individually the two most important variables, the proportion of neighboring grid squares with Argentine ants present, and distance from developed areas. Next, we combined distance to development with the proportion of Argentine ant neighbors in one simulation. Finally, we tested the full best models from previous work (Fitzgerald and Gordon, 2012). The suites of habitat and weather variables included in each full-model simulation differed depending on the season and whether the probability being calculated was for arrival or persistence at a site. Appendix A lists the full models for Argentine ant arrival and persistence in each seasonal transition.

All simulations included random effects of location and year. In addition to the sets of variables listed above, we tested simulations that included only the location and year random effects and no additional information. These effects accounted for variation between locations that was not attributable to habitat features, and variation between years that was not attributable to fluctuations in weather. For each model, the earlier statistical model-fitting procedure calculated adjustments to the intercept for each site and year for which there were data (Fitzgerald and Gordon, 2012). In the simulations, we used these calculated random effects for year, and for grid squares corresponding to survey sites included in the statistical analysis. For each grid square for which random effects had not been calculated during the statistical analysis, we randomly generated a random effect of location, drawn from a normal distribution centered at 0, with standard deviation equal to that of the calculated random effects for the surveyed sites.

2.3.1.4. *Simulations of winter ant distributions used as input for Argentine ant simulations.* The full model simulations for Argentine ant presence at time $t + 1$ depended in part on winter ant presence in at time t. We simulated winter ant occurrences as well as Argentine ant occurrences, and ran winter ant and Argentine ant simulations simultaneously. Winter ant models often depended on Argentine ant presence at time t to predict winter ant presence at time $t + 1$. When a winter ant model included the influence of Argentine ant presence, we used the simulation results for Argentine ants at time t to predict the presence of winter ants at time $t + 1$, and vice versa when a full Argentine ant model included the influence of winter ant presence.

To predict winter ant distributions, we first performed 2 separate simulations for each of the two most important variables from the statistical analysis, vegetation cover and Argentine ant presence during the previous time step (Fitzgerald and Gordon, 2012), then used both of these variables, then the full best models from the previous analysis (Fitzgerald and Gordon, 2012), and finally only random effects as described above.

We used all 25 combinations of the five Argentine ant and five winter variable sets in conjunction with each of the seasonal transitions: fall to fall, spring to spring, and spring to fall and back to spring, resulting in 75 different combinations (Table 1). Each of the 75 different 15-year simulations was repeated 100 times using different randomly generated initial conditions and different site and year effects.

Table 1
Combinations of seasonal transitions, factors used to simulate Argentine ant distributions, and factors used to simulate winter ant distributions. For each set of seasons, each model in the Argentine ant column was paired with each model in the winter ant column. "Full model" refers to the models selected in Fitzgerald and Gordon (2012, Tables 2.1 and 2.2).

Seasons		Argentine ant model		Winter ant model
Fall to fall		Random effects only		Random effects only
		Neighbors with Argentine ants		Vegetation cover
Spring to spring	×	Distance from development	×	Argentine ant presence
		Neighbors with Argentine ants + distance from development		Vegetation cover + Argentine ant presence
Spring to fall to spring		Full model		Full model

2.3.2. Model evaluation

We compared the simulated distribution of Argentine ants with the observed data from field surveys. First, we examined how well the simulations matched the spatial extent of the Argentine ant invasion, regardless of time, to evaluate which model best identified sites where Argentine ants were ever present. We categorized survey sites as "invaded" if they ever had Argentine ants present at any time during the 15 years of field surveys between 1994 and 2009, and as "uninvaded" if they did not. For each simulation run, we found the rate of false negatives, calculated as the proportion of grid squares corresponding to invaded sites at which the simulation predicted that Argentine ants would never be present, and the rate of false positives, calculated as the proportion of grid squares corresponding to uninvaded sites at which the simulation predicted that the species would be present during at least 2 surveys. We also calculated the rate of all errors for each simulation run, as the total proportion of survey sites at which the corresponding simulation results were incorrect.

We then examined how accurately the simulations predicted Argentine ant presence at each particular time at each site, to compare how well the models predicted the changes over time in the ants' distribution. For grid squares and time steps corresponding with survey sites and dates at which Argentine ants were present, we calculated the rate of false negatives, that is, false predictions of Argentine ant absence. For grid squares and time steps corresponding with survey sites and dates at which Argentine ants were absent, we calculated the rate of false positives, that is, false predictions of Argentine ant presence. We also calculated the rate of all errors, the total proportion of survey sites and dates at which the corresponding simulation results were incorrect.

We compared the performance of simulations based on the Argentine ant and winter ant variable sets using a two-way analysis of variance (ANOVA), followed by pairwise *t*-tests with *p*-values corrected for multiple comparisons using the Bonferroni correction. For each measure in each season, we compared the most accurate model from the fall and spring 1-year simulations with the most accurate model from the 6-month simulations, which included both seasons. Statistical tests were performed using R version 2.10.1 (R Development Core Team 2009).

2.3.3. Predicting long-term outcome of Argentine ant invasion at Jasper Ridge

To predict the eventual extent of Argentine ant invasion at Jasper Ridge, we chose the variable set that produced the lowest proportion of false negative predictions of Argentine ant occurrence at particular times. We then performed additional runs of the Argentine ant simulations using this variable set. For the initial conditions of these runs, we assigned Argentine ant presence to all grid squares neighboring the Jasper Ridge boundary, and no Argentine ant presence to all other grid squares. We chose this set of initial conditions based on the assumption that initial propagules entered from developed areas surrounding the preserves (Human et al., 1998). We allowed these models to run for 100 time steps. In 1-year fall or spring simulations, each time step represented one year, and the entire run represented 100 years. In the 6-month

simulation, each time step represented 6 months between spring and fall in odd time steps, or between fall and spring in even time steps, and the entire run represented 50 years. We carried out 100 runs of each 1-year simulation (100 years per run) and each 6-month simulation (50 years per run).

To determine how quickly the Argentine ants approached and then reached their final distribution, we calculated a late-invasion average of the number of grid squares at which Argentine ants were present in each of the last 10 years of the simulation. As a measure of how quickly the invasion approached its long-term distribution, we then determined how quickly the number of grid squares occupied by Argentine ants reached 90% of the late-invasion average. As a measure of how quickly the invasion reached its full long-term distribution, we calculated how many years it took until the number of occupied grid squares first exceeded the late-invasion average. We also compared the predicted Argentine ant distributions, averaged over each set of 100 simulation runs, with the distribution at Jasper Ridge recorded in the last year of the survey data we used, the spring and fall 2009 ant surveys.

2.3.4. Predicting Argentine ant spread at other preserves

We repeated the 50- and 100-year simulations described above for Fremont Older and for Pulgas Ridge. Based on the 100-m ant survey grid at these sites, we simulated a grid of 1-ha squares as we did for Jasper Ridge. For Fremont Older, the simulated grid did not include the western portion of the preserve, which was not surveyed. In the initial conditions for simulations of Argentine ant invasion at Fremont Older, Argentine ants were not assigned to grid squares in boundary areas that bordered the county park, or the western portion of the preserve. For the initial conditions of simulations of Argentine ant invasion at Pulgas Ridge, Argentine ants were assigned to all grid squares at the boundary. For both preserves, random effects were randomly drawn from a normal distribution for every grid square at the beginning of each simulation run, with mean at 0 and standard deviations taken from the random effects calculated for the Jasper Ridge survey sites. To predict future invasions in each preserve, we calculated how quickly the number of grid squares occupied by Argentine ants reached 90% of the late-invasion average, and how soon it exceeded this average. We compared the predicted Argentine ant distributions to the observed distributions from the 2008 to 2009 surveys.

3. Results

3.1. Evaluation of simulations of Argentine ant presence, 1994–2009 at Jasper Ridge

The accuracy of model predictions for Argentine ant distribution depended on the variables used (Tables 2 and 3 and Fig. 1). In full-model simulations, which incorporated information about winter ant presence as predicted by the winter ant simulations, the accuracy of the predicted Argentine ant distributions did not differ significantly depending on which winter ant variable set was in use (2-way ANOVA, N.S.).

Table 2
Error rates (mean ± standard deviation) for predictions of spatial extent of Argentine ant invasion during 1994–2009. Error rates marked with the same letter do not differ statistically from one another (t-tests with Bonferroni corrections, $p > 0.05$). All other pairs of models within the same row differ significantly from one another (t-tests with Bonferroni corrections, $p < 0.05$; for most pairs, $p < 2e{-}16$). Error rates listed in bold are the lowest for that particular measure in that particular season.

Error rates	Full model	Neighbors + development	Development	Neighbors	Random effects
False negatives					
Fall (1 year)	0.073 ± 0.014	0.083 ± 0.014	0.078 ± 0.012	0.106 ± 0.026	0.102 ± 0.017
Fall (6 month)	0.113 ± 0.014	0.077 ± 0.010	**0.071 ± 0.010**[a]	**0.072 ± 0.021**[a]	0.086 ± 0.014
Spring (6 month)	0.174 ± 0.017	0.093 ± 0.012[c]	**0.074 ± 0.011**[d]	**0.074 ± 0.021**[d]	0.092 ± 0.016[c]
Spring (1 year)	0.102 ± 0.016[b]	0.101 ± 0.014[b]	0.100 ± 0.012[b]	0.112 ± 0.025	0.132 ± 0.018
False positives					
Fall (1 year)	0.147 ± 0.028[e]	0.149 ± 0.024[e]	0.153 ± 0.022	0.381 ± 0.080	0.294 ± 0.038
Fall (6 month)	**0.091 ± 0.020**	0.142 ± 0.020[f]	0.141 ± 0.019[f]	0.529 ± 0.084	0.168 ± 0.031
Spring (6 month)	**0.052 ± 0.015**	0.157 ± 0.019	0.175 ± 0.017[h]	0.449 ± 0.082	0.169 ± 0.027[h]
Spring (1 year)	0.126 ± 0.023[g]	0.129 ± 0.022[g]	0.131 ± 0.020	0.273 ± 0.055	0.162 ± 0.026
All errors					
Fall (1 year)	0.102 ± 0.013	0.109 ± 0.012[i]	0.108 ± 0.011[i]	0.209 ± 0.030	0.180 ± 0.018
Fall (6 month)	0.104 ± 0.012	0.103 ± 0.0098	**0.099 ± 0.0096**	0.239 ± 0.032	0.119 ± 0.015
Spring (6 month)	0.117 ± 0.011[k]	0.122 ± 0.011[k]	0.122 ± 0.010[k]	0.236 ± 0.034	0.128 ± 0.015
Spring (1 year)	**0.113 ± 0.013**[j]	**0.114 ± 0.012**[j]	**0.115 ± 0.011**[j]	0.185 ± 0.025	0.146 ± 0.015

3.1.1. Predicting the spatial extent of Argentine ant distribution

Distance to development was the most important factor to predict which sites were ever invaded during the years 1994–2009. Simulations using only distance to development produced the lowest overall rate of errors in identifying which sites were ever invaded in the fall (Table 2, all errors). For spring surveys, distance to development, the presence of Argentine ants at neighboring sites, and full-model variable sets were equally accurate overall in identifying which sites were ever invaded (Table 2, all errors).

Simulations using distance to development and those using presence of Argentine ants at neighboring sites produced the lowest rate of false negative predictions at sites that were invaded at some time during the 15 years (Table 2 and Fig. 1A, false negatives). However, simulations based only on the presence of Argentine ants at neighboring sites often predicted Argentine ant invasion at sites where the ants were never observed during a survey (Table 2 and Fig. 1A, false positives). Full model simulations, which included a range of variables depending on season (see Appendix A), were the least likely to predict Argentine ant invasion at sites where it never occurred during 1994–2009 (Table 2 and Fig. 1A, false positives).

3.1.2. Predicting Argentine ant occurrences at sites at particular times

To predict when Argentine ants arrived at a site, both distance to development and the presence of Argentine ants at neighboring sites were important. Simulations that included these two factors were least likely to predict Argentine ant absence in places and times at which they were actually present (Table 3 and Fig. 1B, false negatives). Among 1-year simulations of fall Argentine ant presence, simulations based only on distance to development and those based on the full suite of variables were similarly accurate, rarely failing to predict Argentine ant presence (Table 3, false negatives). In simulations from 6-month simulations and 1-year spring simulations, the combination of distance to development and presence of Argentine ants at neighboring sites was least likely to fail to predict Argentine ant presence, compared to any other set of variables, including the full model simulations (Table 3, false negatives).

Models based on the full complement of variables were far more accurate than other models in predicting Argentine ant absence (Table 3 and Fig. 1B, fewer false positives). Models based on distance to development, presence of Argentine ants at neighboring sites, or both, were significantly more likely to predict Argentine ant presence where the ants did not occur at a given time than even the random model (Table 3, false positives).

Full models, including all relevant habitat and climate variables, were more accurate overall than models with fewer variables (Table 3, all errors).

3.1.3. Comparison of 1-year and 6-month simulations

Incorporating seasonal effects improved the prediction of Argentine ant distribution. In general, the 6-month simulations made better predictions than the 1-year simulations, both in identifying which sites were ever invaded over 15 years (Table 2) and

Table 3
Error rates (mean ± standard deviation) for predictions Argentine ant occurrences at sites at particular times. Error rates marked with the same letter do not differ statistically from one another (t-tests with Bonferroni corrections, $p > 0.05$). All other pairs of models within the same row differ significantly from one another (t-tests with Bonferroni corrections, $p < 0.05$; for most pairs, $p < 2e{-}16$). Error rates listed in bold are the lowest for that particular measure in that particular season.

| Error rates	Full model	Neighbors + development	Development	Neighbors	Random effects
False negatives					
Fall (1 year)	0.117 ± 0.011[a]	0.117 ± 0.010[a]	0.116 ± 0.008[a]	0.151 ± 0.022[b]	0.151 ± 0.016[b]
Fall (6 month)	0.165 ± 0.012	**0.113 ± 0.008**	0.131 ± 0.008[c]	0.132 ± 0.019[c]	0.156 ± 0.015
Spring (6 month)	0.222 ± 0.013	**0.136 ± 0.009**	0.209 ± 0.009	0.156 ± 0.019	0.199 ± 0.017
Spring (1 year)	0.169 ± 0.016	0.145 ± 0.013	0.159 ± 0.012	0.173 ± 0.025	0.225 ± 0.020
False positives					
Fall (1 year)	0.130 ± 0.012	0.150 ± 0.013	0.142 ± 0.0094	0.167 ± 0.032	0.159 ± 0.016
Fall (6 month)	**0.087 ± 0.007**	0.147 ± 0.0087	0.160 ± 0.008	0.190 ± 0.031	0.124 ± 0.0097
Spring (6 month)	**0.085 ± 0.006**	0.156 ± 0.008	0.204 ± 0.008	0.194 ± 0.029	0.135 ± 0.010
Spring (1 year)	0.137 ± 0.012	0.152 ± 0.012	0.146 ± 0.009	0.167 ± 0.023	0.140 ± 0.012
All errors					
Fall (1 year)	0.124 ± 0.006	0.134 ± 0.0066	0.129 ± 0.0062	0.159 ± 0.015	0.155 ± 0.011
Fall (6 month)	**0.123 ± 0.005**	0.131 ± 0.0055	0.146 ± 0.065	0.163 ± 0.014	0.139 ± 0.0085
Spring (6 month)	**0.144 ± 0.006**	0.147 ± 0.005	0.206 ± 0.006	0.178 ± 0.014	0.162 ± 0.009
Spring (1 year)	0.151 ± 0.008[d]	0.149 ± 0.007	0.152 ± 0.007[d]	0.170 ± 0.012	0.176 ± 0.010
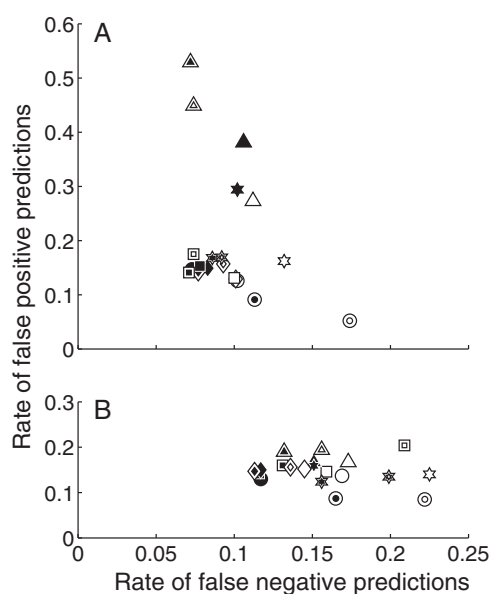
Fig. 1. Error rates for Argentine ant simulations. (A) Spatial extent of Argentine ant distribution. False positive and false negative predictions of whether sites ever had Argentine ants between 1994 and 2009. (B) Argentine ant occurrences at sites at particular times. False positive and false negative predictions of whether sites had Argentine ants at every particular survey between 1994 and 2009. The shapes of the symbols indicate which variables were used in simulations, as follows: triangles for neighbors-only simulations; squares for development-only simulations; diamonds for 2-variable simulations; circles for full-model simulations; and stars for random-effects simulations. Symbol fill indicates season and length of time step as follows: Filled symbols for 1-year fall simulations; plain open symbols for 1-year spring simulations; open symbols surrounding smaller filled symbols for 6-month simulation, fall results; and open symbols surrounding smaller open symbols for 6-month simulation, spring results.

predicting Argentine ant presence and absence at particular sites and times (Table 3). There was one exception: 1-year spring simulation produced lowest rate of errors (Table 2).

3.2. Long-term outcome of Argentine ant invasion at Jasper Ridge

Our long-term simulations of Argentine ant invasion at Jasper Ridge predicted that the invasion would not reach the center of the preserve even after 100 years, but would halt within 400–500 m from roads, buildings, or other development (Fig. 2A). In the simulation results, the invaded area increased quickly, reaching 90% of the long term average in 4–9 years, and first exceeding the late-invasion average at 7–19 years (Fig. 3). After the initial increase, the number of invaded grid squares in each season fluctuated slightly around the long-term mean, with larger fluctuations between the seasons (Fig. 3).

Results for each season in the 6-month simulation were similar to the results for the corresponding season's 1-year simulation, with a late-invasion average of 210 or 208 1-ha grid squares with Argentine ants present each spring, and 234 or 230 1-ha grid squares with Argentine ants each fall, respectively, out of 490 1-ha grid squares tracked in the simulation. Counting only the grid squares corresponding to sites surveyed in spring and fall of 2009, the predicted late invasion averages for spring were 121 1-ha grid squares for both 6-month and 1-year spring simulations. Argentine ants were observed in 105 sites (corresponding to 105 1-ha grid squares) in spring 2009. For fall, the predicted late-invasion averages were 131 or 134 1-ha grid squares for 6-month and 1-year fall simulations, respectively. Argentine ants were observed in 114 sites (corresponding to 114 1-ha grid squares) in fall 2009 (Figs. 2A and D and 3).

3.3. Predicting Argentine ant spread at other preserves

At Fremont Older and Pulgas Ridge, preserves that are smaller than Jasper Ridge, Argentine ants were predicted to reach nearly all grid squares of each preserve (Fig. 2B and C). As at Jasper Ridge, the distributions of Argentine ants at Fremont Older and Pulgas Ridge were predicted to fluctuate seasonally and from year to year. As was also the case for Jasper Ridge, the simulations predicted a more widespread Argentine ant presence than we observed in fall 2008 or spring 2009 surveys. Like those at Jasper Ridge, simulated Argentine ant invasions at Pulgas Ridge and Fremont Older quickly approached their final distribution, although in some simulations the invasions continued to progress slowly for several decades.

Simulation results for Fremont Older predicted that Argentine ants would quickly approach their long-term distribution, reaching 90% of the late-invasion average number of grid squares after 2–7 years. However, in some simulation conditions, the invasion did not reach its full long-term distribution until after several decades. The results from the 1-year simulations predicted that the invasion would first exceed the late-invasion average after 22 years in fall or 39 years in spring. The results from the 6-month simulations were more similar to those at Jasper Ridge, first exceeding the fall late-invasion average after 13 years and the spring late-invasion average after 6 years.

The simulation predicted that Argentine ants would eventually invade most of Fremont Older; however, we did not observe such widespread Argentine ant presence in 2008–2009. The simulation tracked 256 1-ha grid squares at Fremont Older. The 6-month simulation predicted that in years 40–50 of the invasion, a mean of 91% of these grid squares would have Argentine ants present in the fall and 84% would have them in the spring. The 1-year simulations predicted that in years 90–100 of the invasion, 92% of grid squares would have Argentine ants present in the fall and 86% would have Argentine ants in the spring. Out of 172 sites that were surveyed, we observed Argentine ants at 74% in fall 2008, and at 58% in spring 2009. The 6-month and 1-year simulations respectively predicted that Argentine ants would be present at 92% or 94% of the grid squares corresponding to these sites in the fall and at 86% or 88% in the spring.

As at Fremont Older, simulations results for Pulgas Ridge predicted that Argentine ants would quickly approach their long-term distribution, taking 3–7 years to reach 90% of the late-invasion average number of grid squares. Also similar to Fremont Older, 1-year and 6-month simulations differed in their predictions of how quickly the invasion would fully reach its long-term distribution. In the 1-year simulations, the invasion first exceeded the late-invasion average after 34 years in fall or 24 years in spring, while the 6-month simulations for Pulgas Ridge first exceeded the late-invasion averages after 10 years in fall and 8 years in spring

Simulations predicted that Argentine ants would eventually reach most of Pulgas Ridge, but with a lower proportion of grid squares invaded than at Fremont Older. As at Fremont Older, in 2008–2009 we observed Argentine ants at many fewer sites than predicted by the simulation. At Pulgas Ridge, the simulation tracked 179 grid squares. The 6-month simulation predicted that in years 40–50 of the invasion, a mean of 86% of the grid squares would have Argentine ants present in the fall and 79% would have them in the spring. The 1-year simulations predicted that in years 90–100 of the invasion, 84% of the grid squares would have Argentine ants present in the fall and 79% would have the ants in the spring. In this preserve, 112 sites were surveyed in fall 2008 and spring 2009. We observed Argentine ants at 57% of sites in the fall and at 36% of sites in the spring. The 6-month and 1-year simulations respectively predicted that Argentine ants would be present at 91% or 92% of the grid squares corresponding to surveyed sites in the fall and at 85% or 86% of these grid squares in the spring.
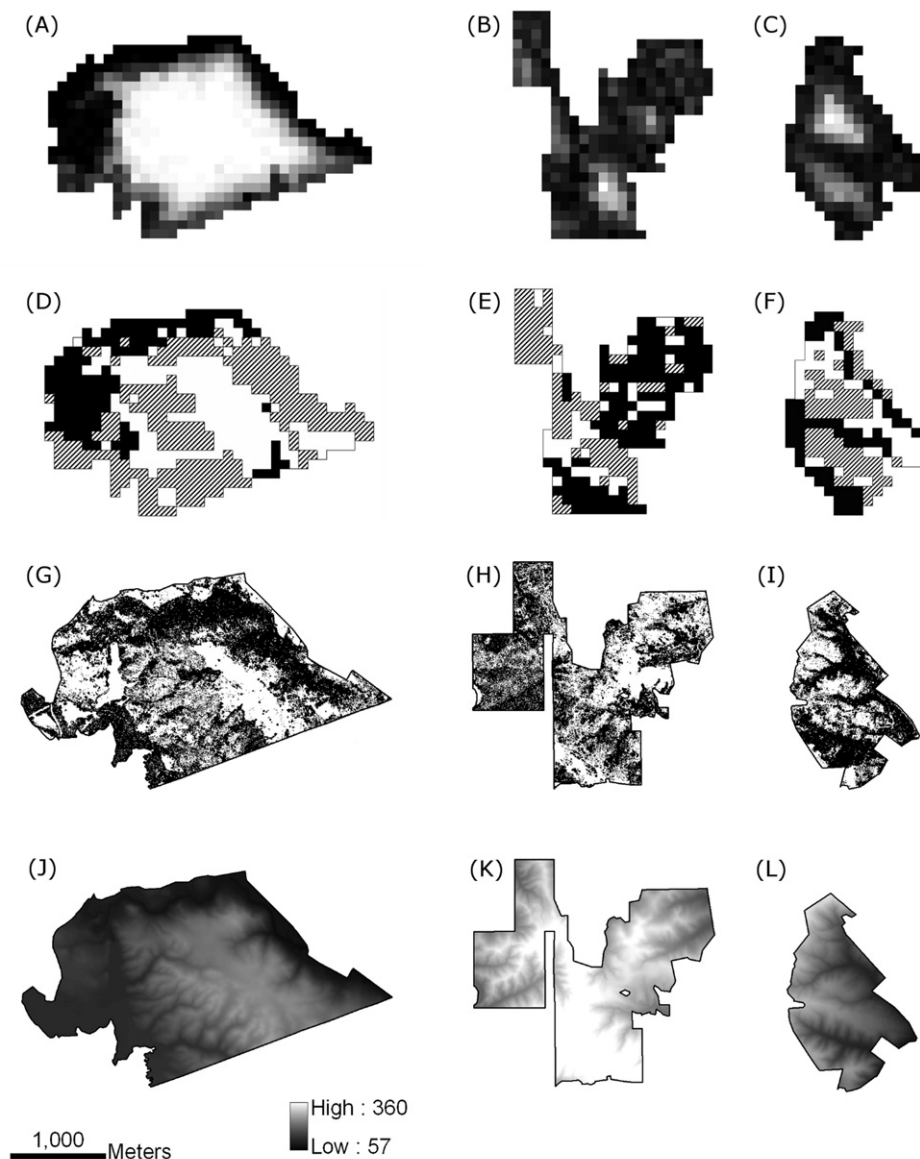
Fig. 2. Predicted Argentine ant distributions, actual distributions, vegetation cover and elevation at Jasper Ridge, Pulgas Ridge, and Fremont Older. A, D, G, J: Jasper Ridge; B, E, H, K: Pulgas Ridge, C, F, I, L: Fremont Older. (A–C) The predicted fall distribution of Argentine ants after 100 years, predicted by distance to disturbance and neighbors with Argentine ants, from one fall to the next. Darker grays indicate that Argentine ants were present in a higher proportion of simulation runs. (D–F) The observed fall distribution of Argentine ants in fall 2009 (D) or fall 2008 (E, F) surveys. Black squares had Argentine ants present, white squares had Argentine ants absent, and striped squares were not surveyed. In panels A–F, each square represents 1 ha. (G–I) Vegetation cover for each preserve. Black areas were covered by trees or shrubs > 0.75 m in height. (J–L) Elevation for each preserve. White areas are higher and black areas are lower (elevation scale is shown below panel J). All maps A–L are shown at the same spatial scale.

4. Discussion

4.1. Distance to developed areas predicts Argentine ant invasion at Jasper Ridge

Our results suggest that Argentine ants in natural areas occur mainly at boundaries with suburban or agricultural lands, in agreement with previous studies (Bolger, 2007; Holway and Suarez, 2006; Suarez et al., 1998). Our previous results also identified distance to developed areas as one of the two factors, along with the presence of Argentine ants at neighboring sites, that were most closely associated with Argentine ant invasion and persistence (Fitzgerald and Gordon, 2012). Here we found that distance to development best predicted whether Argentine ants ever invaded a site over the course of 15 years. Simulations using distance to development were least likely to provide false negatives, predicting

absence at sites where Argentine ants were present. Such false predictions of an invader's absence can be more costly than false predictions of the invader's presence, false positives (Hartley et al., 2006). While false positive errors may lead to a waste of effort on misdirected monitoring and prevention measures, false negative errors may cause an invasion to go undetected and unmitigated.

However, distance to development was not sufficient to predict the time course of the invasion. To predict when a particular site would be invaded, it was also necessary to model the presence of Argentine ants at neighboring sites. Argentine ant dispersal distances by founding queens traveling on foot are estimated to be around 100–150 m per year, at maximum (Ingram and Gordon, 2003; Suarez et al., 2001). Neighboring sites in the survey grid are 100 or 141 m apart, so a site will most likely be invaded over the course of a year only if Argentine ants are already present at neighboring sites.
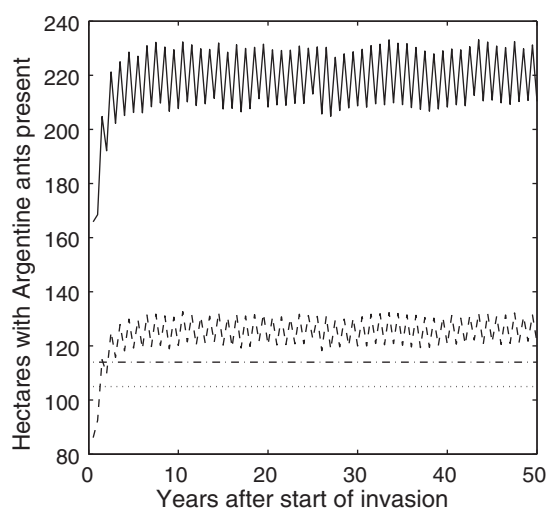
Fig. 3. Long-term predictions for Argentine ant invasion at Jasper Ridge, using the 6-month simulation. Solid line: total number of grid squares predicted to be invaded (out of 490 grid squares total); dashed line: number of surveyed sites predicted to be invaded (out of 331 surveyed sites); dash-dot line: number of sites where Argentine ants were observed in the Fall 2009 survey; dotted line: number of sites where Argentine ants were observed in the Spring 2009 survey.

Development may contribute to invasion as an initial source of propagules, but may also alter the environment in ways that are favorable for the invader. Our simulations assumed that the initial source of propagules for the invasions came from developed areas surrounding the preserves (Human et al., 1998). However, developed areas, including buildings inside preserves, continue to favor Argentine ant establishment even after the initial introduction (Fitzgerald and Gordon, 2012). The effect of human-caused disturbances may be due in part to Argentine ants' ability to exploit areas of cleared vegetation or disturbed soil for nest sites (Carpintero et al., 2003; Way et al., 1997). Distance to development also serves as a proxy for ongoing propagule pressure (Fitzgerald and Gordon, 2012), a factor that is often neglected in invasion models, in spite of a growing recognition of its importance for invasive spread in general (Dullinger et al., 2009; Simberloff, 2009). Further understanding of these effects may allow the formulation of better management decisions at both the boundaries and internal edges of preserves. In the case of Jasper Ridge, the strong association between invasion at a site and its proximity to development explains why the invasion has been stalled since 2000: the remaining uninvaded sites are, for the most part, too far from development to be suitable for invasion.

4.2. Additional factors influencing the time course of invasion

Simulations based on a wider array of habitat and climate variables provided predictions of Argentine ant occurrences that were overall more accurate than those based only on distance to development and Argentine ant presence at neighboring sites, although the extra accuracy was based entirely on the reduction of false positives and did not reduce false negative predictions. Depending on season, the additional factors included various subsets of the following: winter ant presence, vegetation cover, elevation, distance to water, precipitation, and temperature. Simulations based on these full models were less likely than other simulations to predict Argentine ant presence at sites that were not invaded, or at times when Argentine ants were absent. Full-model simulations also offered the lowest overall error rate in predicting the course of the Jasper Ridge invasion through time. However, in a management context, such models might be less useful than simpler ones,

because they required additional data and tended to underestimate the extent of Argentine ant distribution.

Full-model simulations more accurately predicted Argentine ant absence than the simpler ones using only distance to development and the presence of Argentine ants at neighboring sites. At sites in Jasper Ridge where the full models were accurate but the simpler models were not, it appears that Argentine ants had access to the sites but were not established there. These sites were often in closed-canopy forested areas, located at higher elevations, or both (Fig. 2G and J). Similarly, at both Fremont Older and Pulgas Ridge, sites where the simulation predicted invasion, but where Argentine ants were not observed in 2008–2009, often had a high proportion of vegetation cover or were high-elevation sites at the top of a windy ridge (Fig. 2H, I, K and L). Unsuitable microclimate at forested and high-elevation areas may prevent invasion or establishment. Argentine ant populations in Hawaii thrive at elevations up to 2850 m above sea level, but are limited at higher elevations by cool temperatures and heavy rainfall (Hartley et al., 2010; Krushelnycky et al., 2005). The highest elevations in preserves we studied are much lower (from 275 m above sea level at Jasper Ridge and Pulgas Ridge up to 360 m at Fremont Older). However, especially at Pulgas Ridge and Fremont Older, the high elevation areas that were not invaded were located on windy, exposed ridgetops, where temperatures may be much lower, or air and soil may be drier, than in the surrounding habitat. Although Argentine ants readily invade forested sites, they are less likely to maintain a continuous presence under a closed canopy, probably in part due to a cooler microclimate there (Fitzgerald and Gordon, 2012).

At Pulgas Ridge and Fremont Older, we observed Argentine ant presence and absence only during one year, 2008–2009. Because Argentine ant presence fluctuates, especially at forested sites, one observation of Argentine ant absence at these sites does not indicate that the site has never been invaded. Although our simulations overestimated the extent of Argentine ant presence in 2008–2009, they may have been more accurate in their predictions of the eventual extent of the invasion. In addition, our spring surveys in these preserves were conducted earlier in the spring than surveys at Jasper Ridge, and Argentine ants may not yet have begun their spring expansion of territory. We also finished the autumn surveys later in these preserves than at Jasper Ridge, and Argentine ants may have begun their autumn contraction of territory. These factors may account for the discrepancy between model predictions and observed Argentine ant distributions. Additional observations at these preserves, preferably during late May and late September, will be necessary to test this hypothesis.

4.3. Jasper Ridge will continue to provide a refuge to native ants, but smaller preserves may not

Our long-term predictions suggest that the Argentine ant invasion will not reach the central area of Jasper Ridge. Both the 15-year and longer term simulations that used distance to development and dispersal from neighbors overestimated the extent of the invasion at Jasper Ridge. In the long-term simulations, Argentine ant invasion reached its maximum extent after 7–19 years and then stalled. Even after 100 years, Argentine ants were predicted to advance only 400–500 m into Jasper Ridge (Fig. 2A), except in the built-up western area of the preserve, which includes many buildings, roads, and parking lots. These distances are somewhat greater than the 50–250 m Argentine ant edge effects estimated by Bolger (2007) in Southern California. Previous studies have suggested that, unlike in arid Southern California, Argentine ants may more easily invade coastal northern California natural areas (DiGirolamo and Fox, 2006; Holway, 1995). However, our results suggest that even in northern California, the core of natural areas may be resistant to Argentine ant invasion, as long as they are large or isolated enough.

Smaller preserves adjacent to developed areas are more likely to be overrun by Argentine ants. Fremont Older and Pulgas Ridge are considerably smaller than Jasper Ridge. Our long-term simulations predicted that only a few central hectares of each preserve will remain uninvaded (Fig. 2B and C). DiGirolamo and Fox (2006) observed an Argentine ant invasion advancing into the middle of the 242-ha Fort Ord Natural Reserve near Monterey Bay. Fort Ord, like our study areas, is surrounded by development or agricultural areas (DiGirolamo and Fox, 2006). Like Fremont Older, which is of a similar size, Fort Ord may be too small to provide a refuge for native ants. In these preserves, Argentine ants will continue to exert negative effects not only on native ant communities, but also on other native species, including birds and horned lizards (reviewed in Holway et al., 2002). The result here highlights the importance of large preserve size in an urban landscape where invasive species are often abundant in developed lands adjacent to preserves. However, urban conservationists may not have the luxury to ignore invasions into small preserves, and more research will be necessary in order to determine how best to prevent or eradicate these invasions.

4.4. Future use of similar models in other systems

Like habitat suitability models, our model was based on statistical analysis of presence–absence data. However, we combined this approach with elements of cellular automaton models, in order to incorporate the processes of invasion and retreat. This approach allowed us to predict not only the eventual extent of invasion, but also the progress of the invasion over time.

The modeling approach employed here may be useful in predicting other invasions at local scales. This approach is appropriate as long as data are collected on a grid, or a grid can be readily superimposed over the data collection sites, so that it is possible to measure the effect of neighbors on the invader's spread. It may be sufficient to collect data on two occasions from a large number of sites. Finally, this approach does not require any assumption that the invader be at equilibrium with the environment, because it accounts for the process of spread. While this approach does not provide either the large-scale screening capacity of habitat suitability models to identify invasible regions worldwide, or the in-depth understanding of invasion dynamics offered by mechanistic models incorporating more detailed demographic or dispersal parameters, it offers predictions at a local scale, and a measure of invasion limits.

Appendix A. Formulae used in calculating transition probabilities

These formulae are taken from the generalized linear mixed models reported in (Fitzgerald and Gordon, 2012)

Variables

s	random effect of site (adds or subtracts from intercept)
y	random effect of year (adds or subtracts from intercept)
lhn	proportion of neighboring sites with Argentine ants present
dev	distance to developed areas (m)
veg	proportion of 1-ha grid square covered in vegetation > 0.75 m tall
pip	presence of winter ants at a given time step
$elev$	elevation (m)
wat	distance from nearest creek, lake, or marsh (m)
$sppt$	summer precipitation (mm)
$wppt$	winter precipitation (mm)
$stmin$	average summer minimum temperature (°C)
$wtmin$	average winter minimum temperature (°C)
$stmax$	average summer maximum temperature (°C)
$wtmax$	average winter maximum temperature (°C)

Transition probabilities for Argentine ants

A.1. Equations for continuing Argentine ant presence

A.1.1. Effect of Argentine ant presence at neighboring sites
Transition between one fall and the next (1-year simulation):

$$p = (1+\exp(-(s+y-1.1750+5.2814*lhn)))^{-1}$$

Transition between one spring and the next (1-year simulation):

$$p = (1+\exp(-(s+y-0.3171+3.5687*lhn)))^{-1}$$

Transition between spring and fall (6-month simulation):

$$p = (1+\exp(-(s+y+0.4119+4.0767*lhn)))^{-1}$$

Transition between fall and spring (6-month simulation):

$$p = (1+\exp(-(s+y-0.9324+3.7998*lhn)))^{-1}$$

A.1.2. Effect of distance to developed areas
Transition between one fall and the next (1-year simulation):

$$p = (1+\exp(-(s+y+4.9449-0.0210*dev)))^{-1}$$

Transition between one spring and the next (1-year simulation):

$$p = (1+\exp(-(s+y+3.2887-0.0128*dev)))^{-1}$$

Transition between spring and fall (6-month simulation):

$$p = (1+\exp(-(s+y+4.5004-0.0130*dev)))^{-1}$$

Transition between fall and spring (6-month simulation):

$$p = (1+\exp(-(s+y+3.5865-0.0175*dev)))^{-1}$$

A.1.3. Effects of Argentine ant presence at neighboring sites and distance to developed areas
Transition between one fall and the next (1-year simulation):

$$p = (1+\exp(-(s+y+1.1401+3.9287*lhn-0.0130*dev)))^{-1}$$

Transition between one spring and the next (1-year simulation):

$$p = (1+\exp(-(s+y+0.8658+2.9028*lhn-0.0086*dev)))^{-1}$$

Transition between spring and fall (6-month simulation):

$$p = (1+\exp(-(s+y+1.4287+3.5083*lhn-0.0071*dev)))^{-1}$$

Transition between fall and spring (6-month simulation):

$$p = (1+\exp(-(s+y+1.1551+2.5503*lhn-0.0122*dev)))^{-1}$$

A.1.4. Full model (best model from model selection)
Transition between one fall and the next (1-year simulation):

$$\begin{aligned}p = (1 + \exp(-(s+y+11.3944+3.8000*lhn-0.0322*dev \\ -10.3709*veg+0.018406*sppt-0.95*wt\min \\ -0.0419*elev+11.2966*pip+0.0672*veg*elev \\ -2.23*wt\min*pip+0.0046118*dev*wt\min)))^{-1}\end{aligned}$$

Transition between one spring and the next (1-year simulation):

$$\begin{aligned}p = (1 + \exp(-(s+y-7.4764+2.9385*lhn-0.0052*dev \\ -0.5220*pip+0.5005*st\max-12.4540*veg \\ +0.018406*sppt-0.0287*elev-0.0026*wppt \\ +0.0657*veg*elev+0.0059*veg*wppt)))^{-1}\end{aligned}$$

Transition between spring and fall (6-month simulation):

$$\begin{aligned}p = (1 + \exp(-(s+y-10.2568+6.7553*lhn+17.0686*veg \\ -0.0061*dev+0.0137*wat+0.0450*elev \\ +0.8199*st\min-(1.1188e-4)*wat*elev \\ -1.8924*veg*st\min-0.0329*dev*elev)))^{-1}\end{aligned}$$

Transition between fall and spring (6-month simulation):

$$\begin{aligned}p = (1 + \exp(-(s+y+5.5323-0.0097*dev+2.7098*lhn \\ -10.2361*veg-0.0025*wppt-0.0209*elev \\ +0.0056*veg*wppt+0.0469*veg*elev)))^{-1}\end{aligned}$$

A.2. Equations for transition from Argentine ant absence to presence

A.2.1. Effect of Argentine ant presence at neighboring sites
Transition between one fall and the next (1-year simulation):

$$p = (1+\exp(-(s+y-4.0738+5.5548*lhn)))^{-1}$$

Transition between one spring and the next (1-year simulation):

$$p = (1+\exp(-(s+y-4.4938+6.2706*lhn)))^{-1}$$

Transition between spring and fall (6-month simulation):

$$p = (1+\exp(-(s+y-4.0737+6.3606*lhn)))^{-1}$$

Transition between fall and spring (6-month simulation):

$$p = (1+\exp(-(s+y-4.4657+4.7080*lhn)))^{-1}$$

A.2.2. Effect of distance to developed areas
Transition between one fall and the next (1-year simulation):

$$p = (1+\exp(-(s+y+1.2147-0.0145*dev)))^{-1}$$

Transition between one spring and the next (1-year simulation):

$$p = (1+\exp(-(s+y+1.4147-0.0187*dev)))^{-1}$$

Transition between spring and fall (6-month simulation):

$$p = (1+\exp(-(s+y+2.1326-0.0198*dev)))^{-1}$$

Transition between fall and spring (6-month simulation):

$$p = (1+\exp(-(s+y+0.5440-0.0155*dev)))^{-1}$$

A.2.3. Effects of Argentine ant presence at neighboring sites and distance to developed areas
Transition between one fall and the next (1-year simulation):

$$p = (1+\exp(-(s+y-1.1669+3.2221*lhn-0.0087*dev)))^{-1}$$

Transition between one spring and the next (1-year simulation):

$$p = (1+\exp(-(s+y-1.2264+3.5014*lhn-0.0111*dev)))^{-1}$$

Transition between spring and fall (6-month simulation):

$$p = (1+\exp(-(s+y-0.3984+3.2053*lhn-0.0121*dev)))^{-1}$$

Transition between fall and spring (6-month simulation):

$$p = (1+\exp(-(s+y-0.8722+1.9125*lhn-0.0117*dev)))^{-1}$$

A.2.4. Full model (best model from model selection)
Transition between one fall and the next (1-year simulation):

$$\begin{aligned}p = (1 + \exp(-(s+y+21.2602+11.6745*lhn-0.0096*dev \\ -0.8229*ip+(6.7016e-4)*wat-0.7506*sppt \\ +0.2410*wt\min-1.2764*st\min-0.3700*st\max \\ -1.4865*lhn*wt\min-0.0041*lhn*wat \\ +0.0412*sppt*st\min+0.0120*sppt*st\max)))^{-1}\end{aligned}$$

Transition between one spring and the next (1-year simulation):

$$\begin{aligned}p = (1 + \exp(-(s+y+0.1571+5.1729*lhn-0.0089*dev \\ -0.0151*elev+0.5450*veg-3.4504lhn*veg)))^{-1}\end{aligned}$$

Transition between spring and fall (6-month simulation):

$$\begin{aligned}p = (1 + \exp(-(s+y+15.6401+2.7874*lhn-0.0105*dev \\ -0.0159*elev-0.5128*st\max)))^{-1}\end{aligned}$$

Transition between fall and spring (6-month simulation):
(same as model including effects of Argentine ant presence at neighboring sites and distance to developed areas; see A.2.3 above)

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