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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.

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 m^2, 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 m^2 (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,