BIODIVERSITY RESEARCH

The role of abiotic conditions in shaping the long-term patterns of a high-elevation Argentine ant invasion

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ABSTRACT

Analysis of long-term patterns of invasion can reveal the importance of abiotic factors in influencing invasion dynamics, and can help predict future patterns of spread. In the case of the invasive Argentine ant (*Linepithema humile*), most prior studies have investigated this species' limitations in hot and dry climates. However, spatial and temporal patterns of spread involving two ant populations over the course of 30 years at a high elevation site in Hawaii suggest that cold and wet conditions have influenced both the ant's distribution and its rate of invasion. In Haleakala National Park on Maui, we found that a population invading at lower elevation is limited by increasing rainfall and presumably by associated decreasing temperatures. A second, higher elevation population has spread outward in all directions, but rates of spread in different directions appear to have been strongly influenced by differences in elevation and temperature. Patterns of foraging activity were strongly tied to soil temperatures, supporting the hypothesis that variation in temperature can influence rates of spread. Based on past patterns of spread, we predicted a total potential range that covers nearly 50% of the park and 75% of the park's subalpine habitats. We compared this rough estimate with point predictions derived from a degree-day model for Argentine ant colony reproduction, and found that the two independent predictions match closely when soil temperatures are used in the model. The cold, wet conditions that have influenced Argentine ant invasion at this site are likely to be influential at other locations in this species' current and future worldwide distribution.

Keywords

Biological invasions, invasive species, *Linepithema humile*, range limits, rate of spread.

INTRODUCTION

A central goal of invasion biology is predicting where a given species will invade, and in which directions it will spread once established. Understanding how biotic and abiotic factors influence invasion dynamics is integral to this endeavour. Recent work on invasive ants suggests that invasion success in this group is in some situations governed more by abiotic suitability than by biotic resistance, particularly with respect to resistance from the native biota. Although Way *et al.* (1997) provide evidence that some native ant species can limit the highly invasive Argentine ant (*Linepithema humile* [Mayr]) in Portugal, and Majer (1994) hypothesized that native ants might prevent invasion of the Argentine ant in some areas of Western Australia, in many other locations around the world, a handful of invasive ant species have almost entirely displaced native ant assemblages (Holway *et al.*, 2002a). These few invasive ant species appear to share several biological traits that confer substantial competitive advantages

(Holway *et al.*, 2002a), and as a result, resistance from native ants, which are probably their most significant competitors, appears to be less important than environmental conditions in determining where they will invade. In southern California, for instance, Holway *et al.* (2002b) demonstrated that soil moisture and temperature are critical factors influencing invasion success for the Argentine ant, irrespective of native ant richness.

Delineation of the abiotic tolerances of invasive ant species in various climates and habitat types should therefore contribute significantly to our ability to predict future invasion. In Hawaii, the Argentine ant occurs on several islands at elevations ranging from approximately 950 to 2850 m a.s.l. Hawaii has no native ant species (Wilson & Taylor, 1967), and at higher elevations, the Argentine ant often faces no competition from other dominant invasive ant species. It also appears to be free from natural enemies, and provided that food resources are not limiting, abiotic conditions should usually be the only factors governing its spread. In Haleakala National Park (NP) on Maui, two large and

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geographically separate unicolonial populations of the Argentine ant are invading the upper portions of Haleakala volcano. First recorded in 1967, Argentine ants now occupy over 500 ha in the park and adjacent ranchland. The record of Argentine ant invasion at Haleakala National Park is unusual because of its long duration and fine resolution, and represents an excellent opportunity to assess the influence of abiotic variables on the spread of an important invasive species. Ongoing spread at this site is of utmost concern because a number of native Hawaiian arthropod groups, many with member taxa endemic to upper Haleakala volcano, are highly vulnerable to Argentine ant predation or competition (Cole *et al.*, 1992).

We analysed the spatial and temporal patterns of spread of the two ant populations in Haleakala NP from 1967 to 1997. We used available geographical and climate data, and collected additional data regarding the effects of temperature on foraging activity, to assess the roles of these abiotic variables in governing where and how quickly the ant has been invading. Next, we used these findings to predict the total potential range for the Argentine ant in the park, and to estimate how long it would take for *L. humile* to occupy this range. Finally, we compared our predictions against calculations derived from a recently developed degree-day model for Argentine ant reproduction and colony growth (Hartley & Lester, 2003).

METHODS

Study site and organism

Like other highly invasive ant species, the Argentine ant has a unicolonial social structure, forming large, continuous colonies with interconnected nests that exhibit little or no aggression towards one another (Hölldobler & Wilson, 1990). Queens of *L. humile*, unlike those of most ant species, are not known to participate in nuptial flights (Markin, 1970b; Benois, 1973; Passera *et al.*, 1988). Dispersal therefore proceeds via two mechanisms: long distance jump dispersal, and contiguous expansion through budding (Erickson, 1971; Holway, 1995; Suarez *et al.*, 2001). Most of the spread in Haleakala NP has involved budding, but a human-mediated jump dispersal event was almost certainly responsible for initiating a second, higher elevation invasion by introducing propagules from the first. Such unicolonial entities have been referred to as 'populations' (Hölldobler & Wilson, 1990; Krushelnycky & Reimer, 1998; Giraud *et al.*, 2002), indicating groups of nests rather than groups of colonies, or 'supercolonies' (e.g. Hölldobler & Wilson, 1990; Holway *et al.*, 1998; Krushelnycky *et al.*, 2004). Because the latter term has also been used to denote non-aggression among nests separated by large distances and even intervening uninvaded habitat (Holway *et al.*, 1998; Tsutsui *et al.*, 2000; Giraud *et al.*, 2002), we feel that our original usage of 'populations' is more appropriate for the situation at Haleakala. Throughout this paper we refer to the older contiguous invasion at 1900–2375 m elevation encompassing park headquarters as the lower population, and the spatially separate younger invasion encompassing Kalahaku overlook at 2725–2850 m elevation and extending down towards 2200 m elevation within the Haleakala crater as the upper population (Figs 1–3). Three other introduced ant species occur in the vicinity of the two Argentine ant populations in Haleakala NP. However, these species form small colonies that compete little with *L. humile* (see Appendix S1).

The weather on upper Haleakala volcano is largely a product of the predominant northeasterly trade winds, combined with the atmospheric inversion present at roughly 2000–2400 m a.s.l. that traps trade wind flow below it (Giambelluca & Nullet, 1991). These factors dictate rainfall patterns on the mountain, creating a steep rainfall gradient on the northeast slopes below the inversion, with rapidly decreasing rainfall in the southwest,
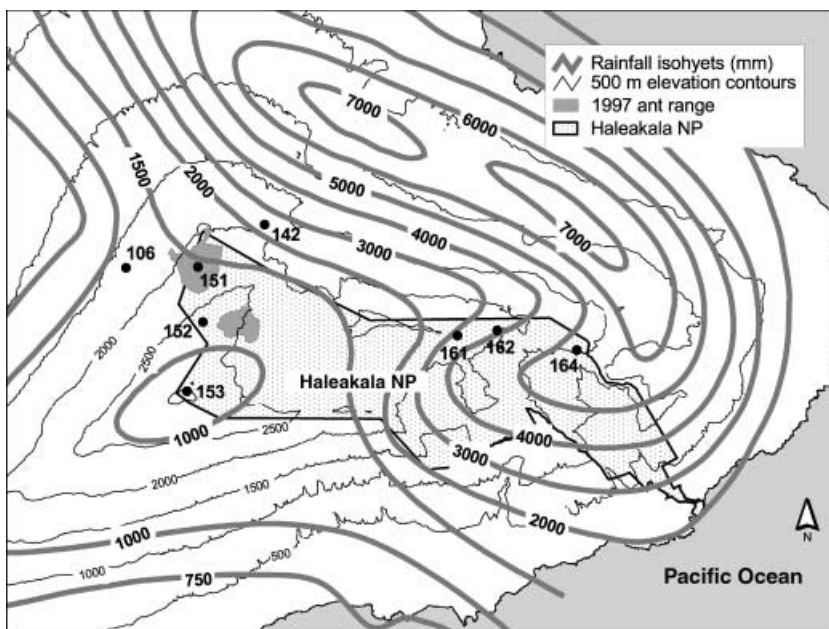

Figure 1 Positions of the lower and upper Argentine ant populations at Haleakala NP relative to the tradewind-generated rainfall pattern of east Maui. Depicted are average annual rainfall isohyets (Giambelluca *et al.*, 1986), as well as locations of climate stations at which degree-day calculations for Argentine ant survival were made (see Methods and Table 2).
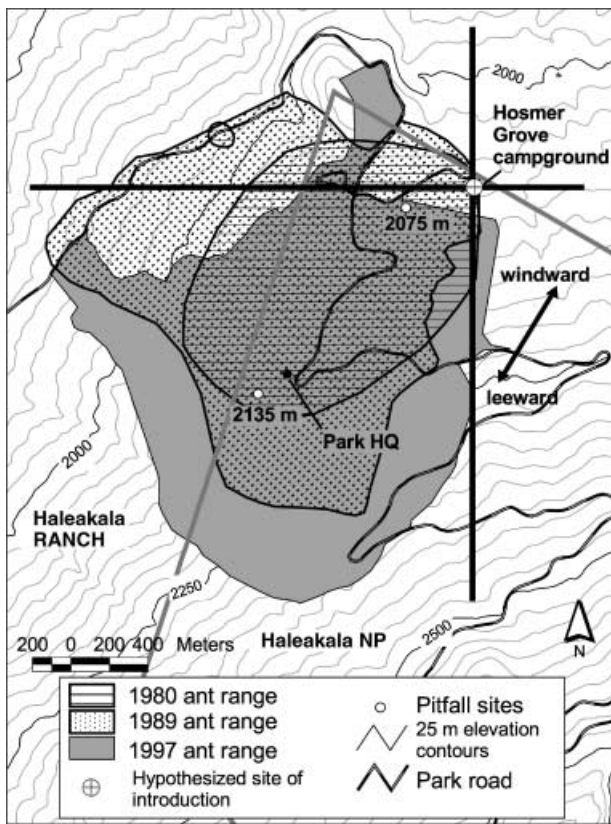
Figure 2 Detail of the lower population showing changes in ant distribution over time. In the interest of visual clarity, we present only the distributions for 1980, 1989 and 1997; distributions for these dates, however, illustrate the important trends. The perpendicular lines centred on Hosmer Grove delineate the main neighbourhood (southwest quadrant) analysed for rate of spread in this population. Also depicted are the two pitfall trapping sites in the lower population (see Methods and Appendix S6), as well as the orientation of the prevailing rainfall gradient.

leeward slopes, and relatively dry air above the inversion (Fig. 1).

The lower Argentine ant population is located in subalpine shrubland. Ground cover approaches 100% of the area between shrubs in the wetter, more windward end of the population, but covers only 25–50% of the ground area between shrubs in the drier, more leeward end of the population. The upper ant population spans a much larger elevational range. At its highest points, outside the crater rim, aeolian habitat predominates, where both shrub and herbaceous vegetation is sparse and the ground consists mostly of bare cinder and rock. Whereas the slope outside the crater rim is relatively moderate (about 15°), the terrain eastward drops off steeply (over 30° to nearly vertical in areas) to the crater floor over 600 m below (Fig. 3). The crater walls and portion of the crater floor occupied by the upper population consist of relatively barren rock screes together with areas of sparse shrub and grass cover.

Huddleston and Fluker (1968) first detected the Argentine ant within Haleakala NP in 1967 at Hosmer Grove, a park campground located at 2065 m elevation (Fig. 2). The date and point
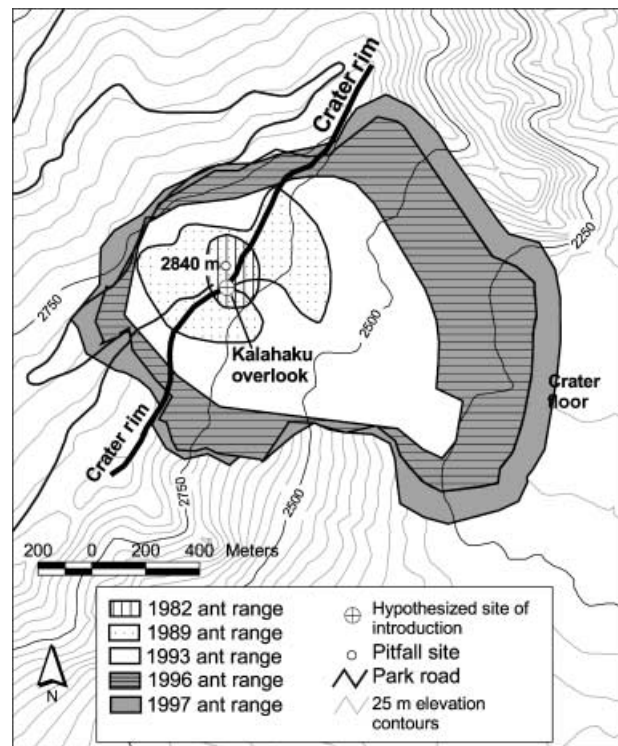

Figure 3 Detail of the upper population showing changes in ant distribution over time. The line following the crater rim separates the two neighbourhoods analysed for rates of spread in this population. Also depicted is the single pitfall trapping site in the upper population (see Methods and Appendix S6).

of introduction will probably never be known conclusively, but the high level of traffic at Hosmer Grove, plus the nature of activities that occur there (picnics, unloading of camping equipment after entry into the park), makes it a likely point of establishment. The upper Argentine ant population was first discovered in 1982 on the rim of Haleakala crater at Kalahaku overlook, a site with a parking lot, a structure and trash cans at 2835 m elevation (G. Fellers & J. Fellers unpublished). At this time, the upper population was apparently recent in origin, totalling about 5 ha in area, and was distributed only around the visitor overlook. Kalahaku overlook is our hypothesized point of introduction for the upper population (Fig. 3). We use these two hypothesized points of introduction in subsequent analyses (see Measuring rates of spread).

Mapping ant distribution

Beginning in 1980, Argentine ants in Haleakala NP have been mapped nine times: in 1980, 1982, 1984, 1989, 1994, 1995 and in 1997 (lower population), and in 1982, 1989, 1993, 1996 and in 1997 (upper population). The methods used to map population boundaries have evolved over time, resulting in substantial improvements in accuracy (see Appendix S2). As a result, area calculations for the earliest distributions in 1980 and 1982 are less reliable. Each of the distributional maps was imported into ARCVIEW version 3.2 for subsequent analyses.

Measuring rates of spread

As in Andow *et al.* (1993), we divided each population into separate neighbourhoods to evaluate rates of radial spread that corresponded to different directions or relevant topographical features. We divided the lower population into four neighbourhoods separated by lines radiating in the four cardinal directions from the hypothesized point of introduction at Hosmer Grove campground (Fig. 2). We chose quadrants based on these compass bearings because the vast majority (94%) of net spread from Hosmer Grove up to 1997 has proceeded southwest. We therefore ignored the minimal spread in the other three quadrants, and calculated the distance of radial spread in the southwest direction only for each year the population was mapped. We made this calculation by converting the areas encompassed within the southwest quadrant of the mapped distributions according to the formula: radial spread = sqrt $(2A/\theta)$, where A is area and θ is the angle in radians over which areal spread was measured (in this case $\pi/2$ radians, or 90°). The population receded somewhat at the northern and northeastern edges of the quadrant after 1989, however, we ignored these losses when calculating rate of radial spread to the southwest.

Spread in the upper population has proceeded in all directions from the hypothesized point of introduction. However, this population has spread much further east and into the crater (83% of total up to 1997) compared to expansion westward outside the crater. We therefore divided the upper population into two neighbourhoods separated by the crater rim (Fig. 3). Radial spread in each neighbourhood was then calculated as for the southwestern portion of the lower population, but in this case θ was π radians, or 180°. All areas used for these analyses were measured as surface areas that accounted for topography. We accomplished this by generating a triangulated irregular network (TIN) from 20 m digital elevation contours using ARCVIEW 3D ANALYST, and then calculating surface areas for the ant populations with the surface tools for points, lines and polygons extension for ARCVIEW (Jenness, 2001).

Abiotic influences on rate of spread

To assess the relative importance of elevation, slope and spatial patterns of rainfall in influencing spatial patterns in rate of spread in each of the two populations, we used analysis of covariance models incorporating these three continuous explanatory variables as well as the categorical covariate, time period. Time period represents each of the time intervals between successive mapping efforts, and was included in the models to control for temporal variation in rates of spread. The explanatory variable elevation cannot, in and of itself, affect an organism. However, we included this variable as a surrogate for linked factors that may influence rate of spread (e.g. temperature, for which we have inadequate spatial data). For these analyses, we used data corresponding to spread in all directions (as opposed to only 90° in the previously described analysis of the lower population) and encompassing the entire temporal record of invasion (1980–1997 for the lower population and 1982–1997 for the upper popula-

tion). All statistical analyses were performed in JMP IN version 3.2.6 (SAS Institute, 1996).

We generated the data for these analyses in ARCVIEW version 3.2 by (1) measuring surface distances to calculate rates of spread (2) interpolating point values for elevation using the elevation TIN described previously, and (3) interpolating point values for rainfall using a TIN created from mean annual rainfall isohyets (digitised versions of those in Giambelluca *et al.*, 1986). These isohyets incorporate some uncertainty, and interpolation between them introduces even more uncertainty. However, these are the best available data for long-term spatial rainfall patterns on Maui, and should be adequate for estimating average rainfall at given locations, particularly on a relative scale. Data consisted of measurements taken along 16 evenly spaced digital compass lines (every 22.5° starting from due N) radiating outward from a central point in each population. For each pair of temporally successive ant distributional shapes in each population (e.g. 1984 and 1989 for the lower population), 16 line segments connected the two boundaries. The lengths of these line segments, divided by the number of intervening years between mapping efforts, resulted in rates of radial spread for this time period. To obtain the corresponding elevation and rainfall data, we averaged the two point values for each variable interpolated at either endpoint of each line segment. We calculated the slope of each line segment as the angle θ using the trigonometric relationship $\sin \theta = $ opp/hyp, where the opposite side of the triangle was the change in elevation between the endpoints of the line segment and the hypotenuse was the surface distance of the line segment. Slope values were coded negative for downhill spread and positive for uphill spread.

The effect of temperature on foraging activity

To assess the importance of temperature variables for describing and predicting ant foraging activity, we collected temperature data in conjunction with ant foraging data for three replicate nests, separated by at least 25 m, in each population. The lower population nests were located at 2175 m elevation and the upper population nests were located at 2825 m elevation. We counted numbers of foraging ants around each nest, in both the presence and absence of an attractive bait, while taking measurements for the following continuous and categorical variables: air temperature, soil temperature (2 cm and 5 cm depth), soil surface temperature, time of day, ground conditions (dry, wet, ice), sky conditions (clear, cloudy, dusk, dark), and whether the ant count was conducted as temperatures were increasing or decreasing on the day in question (warming vs. cooling trend). We counted foraging activity approximately 60 times at each nest (30 baited and 30 unbaited), for a total of 363 foraging counts for the two populations. For a more detailed description of these methods, see Appendix S3.

To compare ant foraging between nests and between counts that were baited versus unbaited, we converted the outcome number of foraging ants to percent foraging activity, by dividing raw ant counts by the maximum observed foraging number for each nest (and also accounting for the baited status of the raw counts). We used analysis of covariance models to assess the

relative importance of the continuous and categorical explanatory variables in influencing foraging activity. Because the four temperature variables were highly correlated, we initially selected only one as the main temperature explanatory variable to avoid multicollinearity, and then explored the effects of subsequently adding other temperature variables. In a second set of analyses, we employed linear regression models using the single best temperature variable in order to predict ant foraging activity (under unbaited conditions only) in the early and late parts of the day. As in Porter and Tschinkel (1987), we found that a function of the form, $\ln(y + 1) = a + bx + cx^2$ (where y is percent foraging activity and x is a temperature variable) best fits the foraging data in both the analysis of covariance and the regression models. For both sets of models, we pooled the data from all three nests in each population.

Other data sources

From 1985 to 1991, relative ant abundance was measured once a year using 18–20 baited pitfall traps at each of three sites (2075, 2135 and 2840 m a.s.l., shown on Figs 2 and 3). The methods used to conduct this trapping are described in Cole *et al.* (1992). We used temperature data from five permanent climate stations situated along an elevational transect from 960 to 2990 m a.s.l. on the western slope of Haleakala. These stations are part of a network of 11 University of Hawaii climate stations in East Maui; data from these stations are posted on the Web (Halenet, 2003). We also used longer-term rainfall data collected at the Haleakala Ranger Station (park headquarters) by the National Climatic Data Center (NCDC, 1980–1997) in order to compare annual rainfall during periods of interest with normal annual rainfall for this location, where normal is calculated as the average from 1951 to 1980.

Assessment of Argentine ant degree-day model

To assess the utility of a recently developed degree-day model of Argentine ant colony survival (Hartley & Lester, 2003), and to independently test our own predictions of future ant spread in the park, we made degree-day calculations on eight of the climate stations in the network referred to previously (shown on Fig. 1). We followed the methods of Hartley and Lester (2003), except that we used hourly average data instead of daily average data. For each climate station location, we made two separate calculations of average number of annual degree-days using two data sets: hourly air temperature, and hourly soil temperature measured as an average between 2 and 6 cm depth with a thermocouple. Hourly soil and air temperature data were available from June 1999 to February 2003, except for a single station, which recorded data from July 2001 to May 2003.

RESULTS

Patterns of spread

Argentine ants were first recorded at Hosmer Grove campground in 1967 (Huddleston & Fluker, 1968). When Fellers and Fellers

(1982) surveyed the area 13 years later in 1980, the population encompassed an area of approximately 165 ha (Fig. 2). The calculated average rate of radial spread from establishment (at Hosmer Grove) to 1980 is therefore ≤ 110 m yr^{-1}. Human-mediated dispersal events subsequent to the original introduction between sites such as Hosmer Grove, park headquarters and the park service area located 1.5 km west of Hosmer Grove could have occurred, and would have the effect of reducing this estimated rate, as would an introduction date earlier than 1967.

The most striking feature of the lower population is that nearly all (94%) of the eventual colonization occurred southwest of Hosmer Grove, or towards the lee of Haleakala volcano. This trend can be seen clearly from 1980 through 1997; spread consistently continued towards the southwest, whereas the population border fluctuated back and forth, or retreated entirely, in the northern and northeastern windward areas (corresponding to a limit of approximately 1600 mm average annual rainfall, Figs 1 and 2). The largest exception to this rule occurred between 1980 and 1982, when the population substantially spread in all directions (not shown). The highest calculated rate of radial spread in the southwestern direction also occurred during this 2-year period (157 m yr^{-1}, Fig. 4). Between 1982 and 1989, the rate of radial spread to the southwest slowed dramatically to roughly 18 m yr^{-1}, and subsequently increased to about 45 m yr^{-1} from 1989 onward (Fig. 4). It is important to note that even if Hosmer Grove was not the initial point of introduction, or if it was one of several early points of introduction, the calculated rates of radial spread after 1980 remain unaffected because these rates of southwestern spread were measured relative to previously mapped population boundaries, and are therefore not dependent on the hypothesized point of introduction. In 1997, the lower population occupied approximately 340 hectares of shrubland both within the park and in adjacent ranchland.

Between the time of its discovery in 1982 and the next survey in 1989, the upper population spread roughly equal distances in all directions, at a rate of approximately 23 m yr^{-1} (Fig. 4). Spreading inside the crater rim (east), however, was slightly faster than outside (west), and by 1993 this discrepancy had
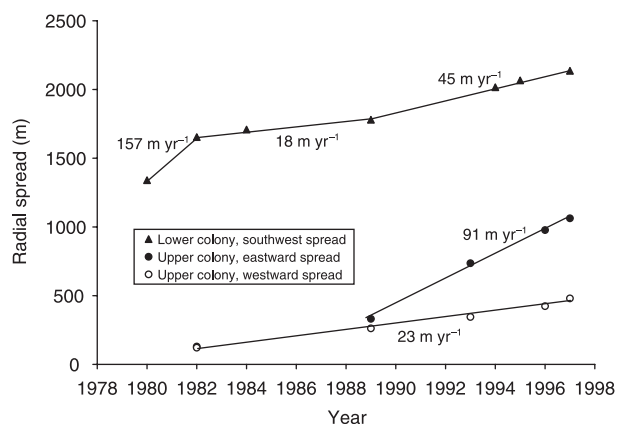

Figure 4 Average rates of radial spread in the three neighbourhoods analysed for the lower and upper Argentine ant populations from 1980 to 1997.

increased dramatically. While westward spread continued at 23 m yr^{-1}, the rate of radial spread towards the east increased to roughly 91 m yr^{-1}, bringing the upper population rapidly down the crater wall to the crater floor (Figs 3 and 4). From 1993 to 1997, average rates of radial spread in both directions continued unchanged, bringing the total area occupied by the upper population in 1997 to roughly 215 hectares. Backward extrapolation of spread prior to 1982 at a rate of 23 m yr^{-1} would place the date of introduction for the upper population in the vicinity of 1977.

Abiotic influences on rates of spread

Rates of spread in the lower population as a whole varied substantially among the different time periods of measurement, and this effect explained the greatest amount of variability in our analysis of covariance model (whole model $R^2 = 0.525$, df = 77, $P < 0.001$; see Appendix S4 for model). After this temporal variation was accounted for, spatial patterns of rainfall had a statistically significant influence on spatial patterns in rates of outward spread, whereas elevation and slope had no significant effect. Specifically, in areas with higher rainfall, rates of spread were lower. While there was multicollinearity between elevation and rainfall ($r = -0.63$), removal of the elevation variable did not significantly change the model ($F_{1,69} = 0.0169$, $P > 0.5$), but removal of the rainfall variable significantly decreased the fit of the model ($F_{1,69} = 7.29$, $P < 0.01$), indicating that these two variables are not interchangeable. In addition, the distribution of spread data was heteroscedastic with respect to rainfall as a result of a consistently narrow range of rates of spread in areas with lower rainfall and high variability in rate of spread in areas with higher rainfall. Uneven variance usually lowers confidence in regression results. However, log-transformation of the spread data yielded very similar results.

In contrast, rainfall and slope had no significant influence on rates of spread in the upper population after controlling for temporal variation, whereas elevation had a strong negative influence (whole model $R^2 = 0.426$, df = 59, $P < 0.001$; see Appendix S4 for model). As elevation increased, rates of spread decreased. Moreover, this effect was strong relative to changing rates of spread over time. The rate of spread data were reasonably homoscedastic in this model, and multicollinearity was low (highest correlation, $r = 0.26$, was between elevation and slope). Spatial autocorrelation was a factor in the spatial data used in the models for both populations. For this reason, we stress the relative importance of explanatory variables, rather than specific predictive values of coefficients. Additional results from experimental manipulation of abiotic variables would strengthen conclusions (e.g. Holway *et al.*, 2002b).

Ant foraging activity in relation to temperature

Descriptive models

In our analysis of covariance models, soil temperature at 5 cm depth provided the most explanatory power among the temperature variables. We removed the time of day variable, as this was highly confounded with soil temperature, and previous studies have shown the Argentine ant to forage round the clock when temperatures are favourable (Markin, 1970a; Human *et al.*, 1998; Witt & Giliomee, 1999). We also discarded all ground condition categorical variables because these were highly skewed: nearly all lower population records were wet, while nearly all upper population records were dry, and there were too few ice data points for analysis ($N = 5$, all at the upper population).

In the lower population, we found that in addition to soil temperature at 5 cm depth, the categorical sky variables (clear, cloudy and dark), the warming or cooling categories, and categorical interactions with temperature provided significant explanatory power (whole model $R^2 = 0.748$, df = 179, $P < 0.001$; see Appendix S5 for model). Cloudy and dark sky conditions decreased foraging activity. The soil surface temperature variable was redundant with the sky variables and was therefore not included, although it provided almost as much explanatory power alone as the sky variables. While baited ant counts were substantially higher than unbaited ant counts, baiting did not significantly influence the relationship between percent foraging activity and temperature. In the upper population, the categorical sky conditions, clear and cloudy were much more effective than soil surface temperature for explaining ant foraging activity, when used in combination with soil temperature at 5 cm depth (whole model $R^2 = 0.726$, df = 182, $P < 0.001$; see Appendix S5 for model). Cloudy conditions decreased foraging, and ants never foraged in the dark at the upper population. The warming versus cooling trend categories were also important, as were interactions between soil temperature and the categorical variables. As in the lower population, baited versus unbaited status did not significantly influence the relationship between foraging activity and temperature.

Predictive models

In our linear regression models, soil temperature at 5 cm depth alone accounted for 76% and 72% of the variation in foraging activity during the first half of the day in the lower and upper elevation populations, respectively (Fig. 5a,b). In the second half of the day, foraging activity often remained relatively high but quite variable as temperatures cooled; activity terminated abruptly in the evening. Consequently, we did not attempt to model the more variable foraging activity at warmer afternoon temperatures, but considered only the final pattern of foraging decline and cessation in the evening: we fitted functions only to data corresponding to temperatures below 15 °C. While soil temperature at 5 cm depth was again the single best predictor of foraging activity in the lower population (Fig. 5c), we found that soil surface temperature was better at describing the slowing and cessation of foraging later in the day in the upper population (Fig. 5d). These two temperature variables individually explained 77% and 57% of the variation in foraging activity at temperatures below 15 °C in the lower and upper elevation populations, respectively.

Using these fitted functions, we calculated the minimum temperature thresholds at which greater than 10% of foraging

Figure 5 The relationships between single temperature variables and ant foraging activity. (a) Lower population warming trend (morning), fitted with the function $\ln(y + 1) = -4.718 + 0.887x - 0.022x^2$ ($R^2 = 0.76$, $P < 0.001$). (b) Upper population warming trend (morning), fitted with the function $\ln(y + 1) = -8.966 + 1.600x - 0.048x^2$ ($R^2 = 0.72$, $P < 0.001$). (c) Lower population cooling trend (evening), fitted with the function $\ln(y + 1) = -24.253 + 4.666x - 0.191x^2$ ($R^2 = 0.77$, $P < 0.001$). (d) Upper population cooling trend (evening), fitted with the function $\ln(y + 1) = -6.120 + 1.575x - 0.061x^2$ ($R^2 = 0.57$, $P < 0.001$). Note that y represents percent foraging activity, whereas x represents soil temperature at 5 cm depth for a–c and soil surface temperature for d.
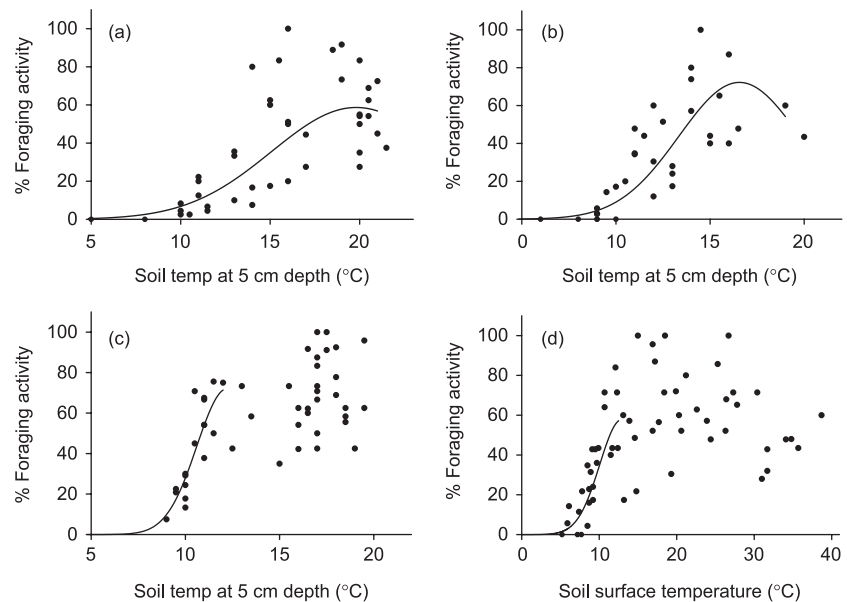
Table 1 Predicted minimum temperature thresholds at which foraging activity exceeds 10% of maximum, based on soil temperature at 5 cm depth

Site	Morning	Evening
Lower population	10.9 °C	9.0 °C
Upper population	10.2 °C	8.9 °C

begins and ends: approximately 9–11 °C (Table 1). We chose this cutoff point because the fitted functions appear less accurate at very low levels of activity (i.e. below 10% of maximum) as a result of fewer data points collected in this range and the ability of one or a few foragers to skew the general pattern of activity. Furthermore, temperature changes fairly rapidly during these periods early and late in the day, and the window of time encompassing all above-ground activity is therefore only slightly longer than that encompassing the top 90%. Although soil surface temperature was better than soil temperature at 5 cm depth for predicting the termination of foraging late in the day in the upper population, we calculated this minimum temperature threshold using soil temperature at 5 cm depth ($R^2 = 0.40$, $P < 0.0001$) instead in order to allow direct comparison with the other three calculated minimum thresholds (Table 1). The tight relationship between soil temperature and time of day also allowed us to estimate, using linear regression functions, when the minimum temperature thresholds for foraging (as defined previously) were exceeded: on average, foraging commenced at about 0935 h ($R^2 = 0.80$, $P < 0.001$) and terminated at about 1930 h in the lower population ($R^2 = 0.81$, $P < 0.001$), while foraging commenced at about 1035 h ($R^2 = 0.69$, $P < 0.001$) and terminated at about 1815 h ($R^2 = 0.65$, $P < 0.001$) in the upper population during the study period.

Table 2 Number of annual degree-days above a miminum temperature threshold of 15.9 °C based on air and soil temperatures at eight climate stations in and around Haleakala National Park†

| Station | Elevation (m) | Annual degree-days | |
		Air temperature	Soil temperature‡
106	1640	92.3	257.4
142	1960	77.7	36.6
151	2120	119.4	434.0
152	2590	63.5	1054.5
153	2990	1.6	540.6
161	2460	11.3	104.3
162	2260	29.3	52.5
164	1650	56.7	0.1

†Climate station locations on Fig. 1.
‡Soil temperature measured as an average between 2 and 6 cm depth.

Argentine ant degree-day model

Hartley and Lester (2003) estimated that the Argentine ant requires 445 degree-days above a minimum temperature threshold of 15.9 °C to complete one generation of development per year. They further designated localities at risk of invasion using a more conservative minimum of 400 degree-days to accommodate for uncertainty in the model and local variation in microsite conditions. Based on soil temperature data and this 400 degree-day minimum, the model predicts that three of the climate station locations in and around Haleakala NP, including the summit of the mountain, are suitable for colony survival (Table 2). In contrast, degree-day calculations using air temperature data predict that the Argentine ant cannot survive at any of the climate station locations. Predictions based on soil temperature therefore reflect the current and near-future ant distribution much more

accurately than those based on air temperature (Fig. 1 and Table 2).

DISCUSSION

A recent review of the worldwide pattern of invasion of the Argentine ant found that it typically colonizes Mediterranean-type climates, as well as some temperate and subtropical regions (Suarez *et al.*, 2001). Most case studies that have investigated the abiotic limits of this species to date have taken place in relatively xeric locales, where moisture availability appears to be the primary limiting factor (Tremper, 1976; Ward, 1987; Majer, 1994; Holway, 1998; Holway *et al.*, 2002b; Walters & Mackay, 2003). In more mesic sites, however, little or no correlation has been detected between water supply and Argentine ant distributional patterns (Way *et al.*, 1997; Human *et al.*, 1998). As this species spreads into more temperate regions, cold temperatures will likely become an increasingly important determinant of invasion success. For instance, recent work predicts that cold temperatures will limit where the ant can invade in New Zealand (Hartley & Lester, 2003). Our results suggest that cold temperatures, resulting in part from high precipitation, are also limiting at high elevation locations in Hawaii.

Range limits

The extreme climatic gradients that exist in Hawaii produce highly variable conditions over short distances. Despite the close proximity of the two Argentine ant populations in Haleakala NP, they are subjected to different climatic forces and have experienced different invasion outcomes. In the lower population, we hypothesize that increasing rainfall, or a covariate of rainfall, has prevented spread northeastward beyond Hosmer Grove in the 30 years since it was first recorded at this site. In the same period, the population has spread uninterrupted toward the south and southwest, a direction that coincides with decreasing moisture along the steep rainfall gradient generated by the predominant northeasterly trade winds.

High rainfall may reduce habitat suitability for the Argentine ant in several ways. First, excessive rainfall may lead to such high soil moisture levels that the ants cannot occupy soil nests. Secondly, high soil and atmospheric moisture may exacerbate effects of low temperature by increasing evaporative cooling, thus pushing temperatures experienced by ants below a critical threshold. Low temperatures can cause mortality or inhibit colony growth (Newell & Barber, 1913; Benois, 1973; Porter, 1988; Hartley & Lester, 2003). Third, much of the precipitation at our study site comes from ground-level clouds that sweep across the mountain from the northeast. These clouds, formed at the atmospheric inversion layer, substantially reduce insolation and decrease both air and soil temperatures. Finally, increasing rainfall indirectly leads to decreasing soil temperature through greater vegetative ground cover. Ground cover composed of grasses, sedges and ferns approaches 100% between shrubs in the more windward areas of the shrubland, and as a result, there are fewer exposed, insolated rocks of the sort that Argentine ants at Haleakala favour

for nesting sites. Some combination of these mechanisms may prevent windward expansion of the lower population beyond areas that receive more than 1600 mm of rainfall per year. As the population spreads towards the drier lee of Haleakala volcano, direct insolation of the soil and rock surface increases as vegetative ground cover and rainfall decrease.

Unlike the lower population, the upper population has not yet encountered environmental conditions that prevent its expansion, although this is likely the highest recorded Argentine ant population in the world. It would seem that the low average annual air temperatures, high winds and occasional snow and ice storms at 2800 m elevation should preclude Argentine ant survival, especially in light of our hypothesis proposing that a combination of increasing rainfall and decreasing temperature has placed colonization limits on the lower population over 700 m below. The upper population, however, benefits from important habitat differences resulting from its position above the atmospheric inversion layer. The air is drier, mean annual rainfall is lower, and ground level clouds are less common (Giambelluca & Nullet, 1991). In contrast to the thick shrubland inhabited by the windward portions of the lower population, the ground surfaces within most of the upper population are largely open, with only sparse vegetation. High levels of solar radiation are therefore absorbed by the dark cinder, soil and rocks, creating a substantial discrepancy between air and soil temperatures, particularly during the warmest parts of the day (Halenet, 2003). Daytime temperatures on the soil surface and just below are often considerably higher than those in the denser shrubland at lower elevations, although temperatures are colder at night and warm for a shorter period during the day (Halenet, 2003). Intense and unobstructed insolation is likely the key to the persistence of the upper population, and may have allowed it to spread in all directions from its point of introduction at 2835 m elevation.

Rates of spread

Given the striking pattern of almost exclusive leeward directional spread of the lower population, we expected that the spatial rainfall pattern on the mountain would be a significant predictor of the spatial pattern in rate of spread (i.e. faster rates in drier areas, slower rates in wetter areas). In contrast, we expected that elevation and slope would explain little of the variation in rate of spread, because the lower population has spread primarily across the mountain, rather than mostly uphill or downhill. These basic predictions were upheld, but in contrast to its apparently strong influence on direction of spread, the spatial rainfall pattern provided weak explanatory power with respect to rate of spread. Temporal variation in rate of spread from 1980 to 1997 dominated our analysis of covariance model, indicating that population-wide changes in invasion rate over time were more important than any spatial patterns (see Appendix S4). One explanation for the weak spatial relationship between rainfall patterns and rate of spread may be that as long as rainfall lies within a tolerable range, rate of spread is relatively unaffected by variation within this range. Another explanation lies in our spatial rainfall data deriving

from long-term trends, which do not account for year-to-year variation. Argentine ants readily move their nests as a result of unfavourable abiotic conditions (Markin, 1970b). The fluctuation observed in the windward, northeastern parts of the lower population border may have resulted from windward spread during dry periods and recession, or mortality during wetter periods, and would have the effect of obscuring much of the relationship between spatial rainfall patterns and rate of spread.

The underlying causes of the two temporal shifts in leeward rate of spread in the lower population between 1980 and 1997 (Fig. 4) are unknown, but changes in ant abundance potentially offer some insight. Pitfall traps in two sites within the lower population recorded a dramatic ant abundance decline at both sites between 1986 and 1988, while no decline occurred in the upper population. It is possible that higher than normal annual rainfall contributed to this decline, which in turn may be tied to the large apparent reduction in rate of spread after 1982. See Appendix S6 for further discussion of this phenomenon.

Haleakala's upper Argentine ant population has spread in all directions since its introduction, but the rate of spread has not been equal in all directions. The relatively slow spread outside the crater rim contrasts sharply with the rapid spread down the crater walls and across the crater floor (Figs 3 and 4). The high rate of spread on nearly flat terrain on the crater floor suggests that rapid transport via rockslides (a function of steep slope) has not been the primary factor influencing the speed of outward population expansion. Instead, it is more likely that as ants invade lower elevation habitat within Haleakala crater, temperatures increase and promote faster rates of spread. Unlike the western face of the mountain, vegetative cover does not increase as elevation decreases on the crater walls and the crater floor (because trade winds are deflected somewhat around the crater perimeter), and soil temperatures at lower elevations in the crater should be considerably warmer than those on the crater rim. This interpretation is supported by the analysis of covariance model, which suggests that elevation, presumably as a surrogate for temperature, is much more important than slope in explaining variation in rate of spread (see Appendix S4). The model also indicates that temporal variation in population-wide rates of spread has been unimportant: most of the variation in rate of spread is accounted for by changes in elevation.

The effects of temperature on ant foraging

Like many other studies (e.g. Talbot, 1943; Markin, 1970a; Bernstein, 1979; Porter & Tschinkel, 1987; Human et al., 1998; Witt & Giliomee, 1999; Holway et al., 2002a), we found that temperature was a primary factor governing ant foraging activity. Soil temperature at 5 cm depth was the most important measured variable influencing foraging in both populations. The relationship between soil temperature and foraging activity was modulated by several additional factors, such as whether skies were clear or cloudy and whether temperatures were warming or cooling. Sky conditions likely influence ant foraging through their fine temporal scale effects on soil surface temperature. Soil surface temperature itself probably provides similar information,

however, this variable has the disadvantage of relatively high collinearity with soil temperature at 5 cm depth. The importance of considering the warming or cooling trend signifies that ant foraging behaviour responds to changing temperature differently depending on whether temperatures are increasing in the morning or dropping in the evening. Surprisingly, we found that the addition of an attractive food resource did not significantly change patterns in percent foraging activity, suggesting that the quality of food resources influences the number of foragers but does not alter the nature of the relationship between temperature and foraging.

Although factors such as sky conditions exert some influence, we found that a single temperature variable alone was effective in predicting foraging activity. Foraging increased relatively evenly throughout the morning in both populations, attaining relatively high levels before noon. Soil temperature at 5 cm depth was the best predictor of this trend, explaining between 72% and 76% of the variance in foraging activity in the two populations. Argentine ant nests at Haleakala are quite shallow, and soil temperatures at a depth of 5 cm may come closest to approximating nest temperatures, and therefore the conditions that dictate when individual ants will become thermally capable of embarking on their first foraging bouts of the day (see Appendix S7). Consistent with our findings at Haleakala, the lower temperature threshold for Argentine ant activity is about 5–10 °C in both California (Markin, 1970a; Human et al., 1998) and South Africa (Witt & Giliomee, 1999).

Throughout most of the remainder of the day, temperature appears to have a lesser influence on foraging activity at Haleakala. Above roughly 14–15 °C (at 5 cm depth), ants foraged easily and overall activity generally stayed at or above 50% of its maximum. This pattern matches the results of Tremper (1976), who found that Argentine ants in the laboratory showed little temperature preference between 17 °C and 33 °C. Biotic signals may in fact be more important than temperature in influencing fine-scale variation in foraging activity above the minimum thermal limits. Trail pheromones leading to food sources or encounters with returning nestmates, for example, may impinge upon temperature stimuli. Relative to that in the morning, foraging in the late afternoon typically continued at a higher level at lower temperatures, and then ceased abruptly (Fig. 5c,d). This pattern may have resulted from biotic signals modulating the effects of temperature until the minimum foraging threshold of about 9 °C was approached. Interaction between biotic and thermal signals could also partly explain why our estimated minimum temperature thresholds were lower in the evening than in the morning in both populations (Table 1).

Total opportunity for foraging and other above-ground activity may be an important factor influencing the Argentine ant's rate of spread. Because temperatures generally decrease with increasing elevation, the window of opportunity for foraging should on average decrease as the Argentine ant colonizes higher and higher areas of the mountain, provided that degree of direct soil insolation is similar. For example, despite responding to temperature in roughly the same way at each of the two sites during our study (Table 1), ants were active approximately 30% longer

(2 h and 15 min) each day at the 2175 m elevation site as compared to the 2825 m elevation site. During months when the Argentine ant is dispersing, this differential may contribute to differing rates of spread across the elevational gradient. While other contributing factors such as survivorship and rates of colony growth are also likely tied to elevation, these data provide a mechanistic explanation supporting one aspect of the relationship between elevation and rate of spread in the upper population.

Predicting future rates and patterns of spread

In 1997, park researchers began an experimental effort to curb the Argentine ant invasion by applying bait and toxicant to the expanding margins of both ant populations. We nevertheless wished to estimate the potential range for this species in the park, as well as likely rates at which it would invade this range if left unchecked. These estimates would serve as a rough benchmark against which to assess management success.

Previous efforts to estimate potential ranges for another invasive ant, *Solenopsis invicta* Buren, have used climatic variables such as air or soil temperature and rainfall to either determine suitable combinations of these variables based on past colonization trends (Pimm & Bartell, 1980), or to model colony growth and survival thresholds (Korzukhin *et al.*, 2001 and others reviewed therein). Taking a related approach, Hartley and Lester (2003) constructed a degree-day model for successful colony growth of the Argentine ant based on rates of development in the laboratory, and then used this model to estimate the ant's potential range in New Zealand. In these and other climate-matching approaches (e.g. Hoddle, 2004), point data from individual climate stations can often be taken to approximate the conditions between the points when evaluating total potential range. On a large scale, such as the continental United States in the case of *S. invicta*, this resolution is highly informative. In our situation, where prediction of fine-scale distributional change was the goal and where the number and geographical coverage of climate stations was inadequate, a more ad hoc approach was necessary.

Much of our target area (the national park) lies within the range of abiotic tolerances already known to be suitable for the Argentine ant. We therefore estimated a total potential range by first assuming that all areas in the park under 2850 m elevation and receiving less than 1600 mm of rainfall per year were at risk, as these areas are currently being invaded without difficulty. Desiccation in hot, dry areas has been cited as a major limiting factor in areas such as southern (240 mm rainfall/year) and central California (250–380 mm rainfall/year) (Tremper, 1976; Holway *et al.*, 2002b). Because all areas in the park experience considerably more rainfall, we did not expect xeric conditions to play a role in shaping the total potential range. Soil type is another factor potentially limiting spread of the Argentine ant in Portugal (Way *et al.*, 1997), but we disregarded this variable because both populations have invaded various lava flow types and ground substrates in the park. Next, we predicted that the remaining area to the summit would eventually be invaded as

well, as the upper population is still spreading uphill, albeit slowly, and the summit is only about 200 m higher in elevation. Finally, we extended the predicted range somewhat further eastward into areas of higher rainfall and lower elevation. We included these areas based on (1) the hypothesis that insolation of relatively open-ground habitat can compensate for higher moisture levels, particularly as elevation decreases, and (2) the fact that another unicolonial, highly invasive ant species (*Pheidole megacephala* [Fabricius]) has already been able to invade some of the areas in question. This species typically thrives at lower elevations in Hawaii, is not known to favour wet habitat (Reimer, 1994), and as such is presumably less cold-tolerant than the Argentine ant.

The resultant potential range map covers roughly 5360 ha within the park. This constitutes about 48% of the total park area, and approximately 75% of the subalpine shrubland and aeolian zone habitats. This admittedly crude estimate would benefit substantially from additional information on the relationships between elevation, rainfall and soil temperature as they relate to microhabitat suitability, and from more complete spatial data for the latter two variables. In addition, biotic factors such as food resource scarcity may very well influence microhabitat suitability throughout parts of this predicted range, and could also be incorporated.

When we independently tested the Hartley and Lester (2003) degree-day model at the few locations in and around the park where climate data are available (see Fig. 1), the results calculated from soil temperatures match our predictions as well as current distributional patterns. For instance, the model correctly determines that the Argentine ant can survive at 2120 m and 2590 m elevations on the west slope of Haleakala, and further predicts that it will colonize the summit. It suggests that temperatures at the climate station near park headquarters (151), in the centre of the lower population, are only marginally warm enough to support Argentine ant reproduction, and that more open sites upslope are more suitable. Consistent with our total projected range, the model predicts that the wet, northeast slope of Haleakala is too cold for Argentine ant colonization. Even the treeless and shrubless ranchland surrounding climate station 106, located below the park and the lower ant population, may be too cold for Argentine ants because of thick grass cover. Not only would this explain the slow westward spread of the lower population after it reached areas with dense grass, but it implies that Argentine ants will be unlikely to secondarily invade the park from residential areas further down the mountain without human-assisted dispersal over the intervening cattle pastures.

How long would it take the Argentine ant to realize this potential range? The two populations appear to have spread at relatively steady rates within larger scale neighbourhoods for significant periods of time between 1980 and 1997 (Fig. 4). Ants spreading outside the crater rim in the upper population, for instance, have averaged a rate of 23 m yr^{-1} for the entire 15 years on record. The portion of the upper population spreading into the crater, as well as leeward spread in the lower population, have averaged 91 m yr^{-1} and 45 m yr^{-1}, respectively, over the last 9 years on record. These apparent linear rates of radial spread

over significant time periods indicate exponential growth in area, and are consistent with the diffusion model of spread (Skellam, 1951; see Appendix S8). Working under the assumption that these rates would have continued unchanged in their respective neighbourhoods without management intervention, we calculated that the two populations would have merged in less than 20 years (from 1997), would invade half of the predicted total range in the park in 30 years, and would cover roughly 90% of this area in about 70 years. This exercise also emphasizes the overwhelming effect of secondary jump-dispersal on overall invasion rate (Holway, 1995; Suarez *et al.*, 2001): we estimate that the establishment of the second population at Kalahaku around 1977 has accelerated the invasion process into the park by about 50–60 years.

CONCLUSIONS

Together, the two Haleakala Argentine ant populations highlight several important points. First, the patterns of spread clearly demonstrate that this species is not restricted to areas of human disturbance. The vast majority of the two populations occupy habitat unaffected by roads, trails or structures. Second, rainfall and soil temperature may interact, through mechanisms such as the ones outlined here, to become the overriding factors dictating where this species can invade in cooler, wetter climates. As in Liebhold *et al.* (1992), abiotic factors may also influence the rate of invasion. Finally, as more invaded sites are studied, predictions of world-wide potential range for invasive species will become stronger. Sites that reveal natural range limits are particularly valuable for testing and refining climate-based predictive models. For example, additional soil temperature data currently being collected at Haleakala should help make the patterns at this site apply more directly to worldwide Argentine ant invasion predictions.

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SUPPLEMENTARY MATERIAL

The following materials are available online at www.blackwell-synergy.com/loi/ddi

Appendix S1 Additional ant species occurring at the study site

Appendix S2 Detailed methodology for mapping ant distribution

Appendix S3 Details of foraging activity data collection methods

Appendix S4 Analysis of covariance models for rates of spread

Appendix S5 Analysis of covariance models for foraging activity

Appendix S6 Changes in ant abundances and implications for rates of spread

Appendix S7 Diurnal and seasonal dynamics between temperature and foraging

Appendix S8 Ant spread under the diffusion model

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