The widespread collapse of an invasive species: Argentine ants (Linepithema humile) in New Zealand

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Invasive ants are a substantial global problem for biodiversity [6]. However, populations of other invasive species have occasionally been known to collapse [10]. Similarly, our long-term personal observations of local Argentine ant infestations also suggested that not all populations are persisting within New Zealand. Here, we asked three questions. Firstly, are Argentine ant infestations persistent, and if not, how is the collapse of these populations influenced by temperature and rainfall? Secondly, how might climate change affect the survival of Argentine ant populations? Finally, do Argentine ants reduce species richness and change resident ant communities, and do these communities recover after the collapse of Argentine ant populations?

2. MATERIAL AND METHODS
Using records of first recorded Argentine ant presence [5], we examined 150 locations across this ant’s range in New Zealand. Ant communities were surveyed on the North and South Islands in January and February 2011. Detail on the sampling sites is given in the electronic supplementary material, S1. A GPS unit was used to navigate to the original location (+10 m) where the surrounding area of approximately 200 × 200 m was hand-searched for ants. Such survey methods are considered effective for ant sampling [11]. Ants were collected with aspirators and preserved for identification. Climate data (annual rainfall (millimetre), mean temperature (°C), mean maximum daily temperature (°C) and mean minimum daily temperature (°C)) [5] were obtained from http://clidfl.niwa.co.nz for the nearest weather station to each sampling site, which was within approximately 20 km of each location. Cox’s Proportional Hazards (PH) models were used to test the influence of the four climate variables on the rate of disappearance of Argentine ant populations. Two parsimonious models were suggested by a forward stepwise model selection algorithm, one of which is presented here. Model 1 had two main effects: total rainfall and mean maximum daily temperature. For presentation, the survival data were organized into four groups based on the medians for rainfall and mean maximum temperature. A Kaplan–Meier Survival Curve and Logrank statistic were used to estimate survival and compare groups. For further details on model selection and climate groupings (S2), see the electronic supplementary material.

To create our climate change model, we applied the Cox’s PH survival model fitted to current and future climate data to estimate probabilities of colony persistence under local conditions of rainfall and mean maximum daily temperature. Data regarding the climate across all of New Zealand were obtained from www.worldclim.org. Current climate was described by the 1950–2000 monthly averages at 2.5 min resolution, while for future climate we used predictions for 2050 generated by the CSIRO A2 model. See the electronic supplementary material for details on the CSIRO A2 model.

Auckland sites were selected to examine the effects of Argentine ants on communities, owing to the high diversity of its ant communities and the considerable length of time Argentine ants had been present. Three types of Auckland communities were assessed and compared for differences in species richness and community composition: (i) communities currently with Argentine ants; (ii) communities where Argentine ant populations were no longer detected; and (iii) communities where Argentine ants had never been recorded as present. The species richness of the three types of Auckland ant communities was examined using an ANOVA. To examine differences in the species composition between these communities, we used multivariate data analysis in Plymouth Routines in Multivariate Ecological Research (PRIMER, v. 6.1.11, 2008: Plymouth Marine Laboratory, UK). An ordination analysis was conducted using non-metric multi-dimensional scaling (MDS) plots that score communities based on their similarity or dissimilarity. The resemblance matrix was measured using Jaccard similarity coefficients, which use presence/absence data. Stress values on MDS plots below 0.2 are an indication of a good fit. A distance-based test for homogeneity of multivariate...
dispersions (PERMDISP) was used to assess the differences in species composition between the groups on the MDS plot using 9999 permutations.

3. RESULTS

Argentine ant populations had collapsed in 60 of the 150 locations. Of the Argentine ant populations that did remain, many had shrunk from numerous nests covering multiple hectares with extremely high abundances to just one or two nests covering a very small area with low worker densities. A Kaplan–Meier estimator found the time to collapse was negatively influenced by mean maximum daily temperature and positively influenced by total annual rainfall ($p < 0.001$). Mean time to population collapse of these ants ranged from 10.48 years (10.10–10.86 years; 95% CI) in conditions of low rainfall and low temperature, to 17.80 years (15.59–20.01 years) under conditions of low rainfall and high temperature (figure 1a and table 1).

Climate change was predicted to increase the probability of Argentine ant survival in many regions (figure 1b,c). Under the CSIRO A2 model, the area of New Zealand in which populations have a greater than 80 per cent chance of surviving for 15 years or more increased from 0.26 to 1.29 per cent. Nowhere did survival probability decrease with climate change. Ant species richness was significantly affected by the presence of Argentine ants ($F_{2,58} = 6.041, p = 0.004$; figure 2a). Post hoc Tukey tests showed that the ant communities with Argentine ants had significantly fewer ant species than communities without Argentine ants. The species richness of ant communities after Argentine ant collapse was intermediate, likely indicating that the communities were at various stages of recovery post Argentine ant collapse. Communities with Argentine ants had significantly different community composition from those without Argentine ants present (PERMDISP; $t = 5.359, p < 0.001$) and from communities where populations had collapsed (PERMDISP; $t = 3.119, p < 0.001$; figure 2b). In contrast, communities where Argentine ants had collapsed were indistinguishable from those which had never been invaded (PERMDISP, $t = 0.615, p = 0.596$).

4. DISCUSSION

Argentine ants had disappeared from 40 per cent of our sampling sites. In many other sites, Argentine ant populations had been reduced from occupying multiple nests encompassing large areas to one or two small nests in a few square metres. These results are consistent with our observations of the slow shrinkage and disappearance of large Argentine ant infestations in areas, such as Wellington. They do not appear to move and to our knowledge are not managed by humans in any way that might reduce their abundance.

The shrinking and eventual disappearance of invasive species populations, including invasive ant populations, has historically been observed elsewhere [3]. For example, yellow crazy ant (Anoplolepis gracilipes) populations in the Seychelles declined dramatically over time and in some areas disappeared [10]. The reasons

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Table 1. Kaplan–Meier estimates of survival time of Argentine ant populations under four different climate regimes.

<table>
<thead>
<tr>
<th>climate regime</th>
<th>n</th>
<th>time (years)</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>low rainfall–low temperature</td>
<td>50</td>
<td>10.5</td>
<td>10.1–10.9</td>
</tr>
<tr>
<td>high rainfall–low temperature</td>
<td>34</td>
<td>12.4</td>
<td>11.0–13.7</td>
</tr>
<tr>
<td>low rainfall–high temperature</td>
<td>22</td>
<td>17.8</td>
<td>15.6–20.0</td>
</tr>
<tr>
<td>high rainfall–high temperature</td>
<td>44</td>
<td>13.0</td>
<td>11.0–15.0</td>
</tr>
<tr>
<td>overall</td>
<td>150</td>
<td>14.1</td>
<td>12.9–15.3</td>
</tr>
</tbody>
</table>

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Figure 1. (a) Survivorship curves for Argentine ant populations, with data divided into subsets of high and low temperature and rainfall conditions. (b) Probability of Argentine ant incursions surviving for 15 years or more under current climate conditions, and (c) after the CSIRO A2 climate change predictions.
for the population collapse of Argentine or yellow crazy ant populations are not yet known. However, population genetics predicts that invasive species might collapse owing to inbreeding depression or an inability to adapt to their new environment [12]. Previous genetic studies have revealed that the New Zealand population of Argentine ants has among the lowest recorded genetic diversity of any introduced Argentine ant population worldwide, indicative of the entire supercolony having arisen from an incursion of just one nest [7,12]. Low genetic diversity, perhaps in combination with pathogens [13] or a depletion of local resources [10], is a candidate mechanism for these collapses.

Our results indicate that the survival of Argentine ant infestations is negatively influenced by increasing rainfall and positively influenced by increasing temperature, which is in agreement with previous work [5,9]. Consequently, our survival model, when applied to future climate data, indicates increased survival times in all parts of the country. The total New Zealand area with a higher than 80 per cent chance of having populations survive 15 years or more substantially increases from 0.26 (69 685 km2) to 1.29 per cent (345 747 km2). However, we note that, even under current conditions of high temperatures and low rainfall, the probability of Argentine ants persisting more than 20 years was less than 20 per cent (figure 1a). While climate change may increase persistence, this increase in persistence is not dramatic.

Argentine ants are well known to competitively displace other ant species [6], but we found 61 per cent of sites where Argentine ants were still present to have other ant species living side by side. Many of these populations had shrunk to tiny remnant populations with multiple ant species present at the same site. In places where Argentine ants were at very high abundances there were very few or no co-occurring ant species, but at sites where Argentine ant densities were low there were many other ant species. When present in low abundance, Argentine ants are less competitive and prone to local extinction [14]. Thus, any process that reduces Argentine ant densities (such as pathogens) is likely to have compounding effects on the ability of these invasive ants to persist. Impacts may also lessen over time and interact with climate [8]. Other ant species re-colonized all areas where Argentine ant populations had collapsed. Our community analysis suggests ant communities that were formerly invaded by Argentine ants are recovering and regaining their pre-invasion structure.

Given the local presence of this invasive species for short durations of 10–20 years, and the apparent recovery of the resident communities after their collapse, it seems that the long-term ecological or evolutionary effects of Argentine ants in New Zealand may not be as dire as first feared. The control of Argentine ants was predicted to cost New Zealand up to $68 million per year [15]. Such economic and environmental costs will be considerably smaller here and in other countries, however, if populations collapse on their own accord. Other invasive species and climate change clearly contribute to the current global biodiversity crisis [1], and their costs may be substantial. Determining which species are susceptible and the mechanisms for these collapses should be a high priority for invasion biologists.

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3 Simberloff, D. & Gibbons, L. 2004 Now you see them, now you don’t!—population crashes of established introduced species. Biol. Invasion 6, 161–172. (doi:10.1023/B:BINV.0000022133.49752.46)