Relative risk of invasive ants (Hymenoptera: Formicidae) establishing in New Zealand

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Abstract  Human-assisted spread of species poses a major challenge to border security agencies. Ideally, limited resources need to be targeted at species posing the most risk. Climate matching is an important component of assessing risk but often little or no biological information is available to enable detailed modelling. To assess if distribution records alone provide useful establishment predictions we compare the climate in New Zealand and its outlying islands to that found in the current native and introduced ranges of 12 tramp ant species, three of which are already established in New Zealand, using the climate module of BIOSECURE, a risk assessment tool. Eleven species showed a similar general pattern, with mean annual temperature being the climatic variable with the least overlap between the estimated realised niche and the predicted New Zealand niche. The twelfth species, of temperate origin, is less restricted by temperature, but much of New Zealand may have too high a rainfall. The present and future threats posed by tramp ants are discussed in relation to climate limitations.

Keywords  Anoplolepis gracilipes; climate matching; Lasius neglectus; Linepithema humile; Monomorium destructor; M. pharaonis; Paratrechina longicornis; Pheidole megacephala; risk assessment; Solenopsis geminata; S. invicta; S. richteri; Tapinoma melanocephalum; temperature; tramp ants; Wasmannia auropunctata

INTRODUCTION

With the enormous volumes of trade and movement of people between countries, there is frequent human-assisted spread of species beyond their native range (Van Driesche & Van Driesche 2004). This poses a major challenge to border security agencies (Maynard et al. 2004). There are limited resources available to respond to every incursion so priority setting is necessary, using some form of risk assessment (Ruesink et al. 1995; Kolar & Lodge 2001; Stohlgren & Schnase 2006). An important component of assessing risk is determining the potential of a species to establish populations in the local climate (Stohlgren & Schnase 2006).

Ants are common stowaways on international freight, and have established beyond their native range on numerous occasions (e.g., McGlynn 1999). For most taxa there is limited biological information, beyond scattered distribution records, on which to base species range predictions.

In New Zealand there have been frequent interceptions of ants at the border (Ward et al. 2006). Of those arriving, about 28 species are confirmed to have established (Berry et al. 1997; Ward 2005; Harris & Berry 2001), a significant addition to the depauperate native ant fauna of around 11 species (Valentine & Walker 1991). For many of the introduced species, New Zealand is the only place they have established outside their native range (McGlynn 1999; Harris & Berry 2001). Others that have established in New Zealand are “tramp” species (sensu Passera 1994) and include predominantly urban pests (e.g., Monomorium pharaonis (Forel)) and those that have documented impacts in urban and native.

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systems, e.g., *Linepithema humile* (Mayr) (Human & Gordon 1997; Suarez et al. 2000) and *Pheidole megacephala* (Fab.) (Hoffmann et al. 1999).

Incursions of tramp species into New Zealand continue. Since March 2001 nests of *Solenopsis invicta* Buren (three sites), Paratrechina longicornis (Latreille) (at least three sites), *Anoplolepis gracilipes* (F. Smith) (two sites), *S. geminata* (Fab.) and *Tapinoma melanocephalum* (Fab.) have been found near airports, sea ports or facilities receiving imported cargo (S. O’Connor Biosecurity New Zealand pers. comm. 2006). None of these species have established, as Biosecurity New Zealand has made a considerable effort to eradicate each incursion.

New Zealand has a cool temperate climate and it is unclear which of the species being intercepted would pose a risk of establishment if no management was undertaken. Most established adventive ant species have restricted northern distributions; few adventive species survive outside urban areas in the lower North Island and South Island (Anon. 2005).

One of the main factors influencing establishment of new ant species in New Zealand is likely to be species-specific responses to abiotic factors such as climate. Temperature can regulate ant colony foraging activity (Vogt et al. 2003), oviposition rates (e.g., Newell & Barber 1913 cited in Vega & Rust 2001), development of brood (Porter 1988), nest site selection (Chen et al. 2002), and extremes of temperature can kill adults or whole colonies (Korzukhin et al. 2001).

Ants do not forage during heavy rain, and in high rainfall areas foraging time is reduced and possibly so also is the probability of establishment (Cole et al. 1992; Vega & Rust 2001). In high rainfall areas it may be the permeability of the soil and the availability of relatively dry areas to nest that limits distribution, rather than rainfall per se (Chen et al. 2002). Conversely, in arid climates, a lack of water probably restricts the distribution of ants such as *L. humile* (Ward 1987).

Is it possible to ignore the arrival of some species at a border, confident that they are unable to establish in the local climate, and focus effort on those where establishment is likely? The present contribution addresses this question by providing an assessment of the risks of exotic ants establishing in New Zealand using a climate envelope approach. We focused on ant species identified as potential threats to New Zealand (Harris et al. 2005), all with documented impacts in other parts of the world, including several with recent histories of incursion into New Zealand. To test the validity of the climate envelope approach, we also assessed predictions for three tramp ant species already established in New Zealand. Analyses were performed using the climate module of a risk assessment tool BIOSECURE (Barker et al. 2003) to distinguish those species that have a low likelihood of establishment from those that are likely to find New Zealand urban areas favourable, and those that pose a risk to native habitats.

**METHODS**

New Zealand administers island groups extending from the Kermadec Islands in the South Pacific (the largest being the 2941 ha Raoul Island; 29°15’S, 177°55’W) to the subantarctic Campbell Islands (52°33’S, 169°09’E) so they represent a wide range of climates (Appendix 1).

Twelve ant species that have established outside their native range were recognised as of interest to New Zealand and thus included in our assessments (Table 1). Records of species distribution were obtained from the scientific literature, ant collections records available on the internet, from communication with researchers, and from specimen labels associated with museum collections. Generally, fewer data were available from the native range than the introduced range of individual species, with *S. geminata* and *Wasmannia auropunctata* (Roger) being the exceptions. Records from a specific collection locality for which robust geographic coordinates could be derived were preferred for modelling, and indeed constituted the bulk of the data used. For mainland United States, some county occurrence records were used, with the county capital taken as the locality for which a geographic coordinate was derived. For some oceanic islands presence records were used, and a coastal town was used as the locality. Data points were segregated into those pertaining to the species’ native range and those associated with the introduced ranges. Within the introduced range, records documented as being closely associated with buildings (e.g., found in heated glasshouses in temperate regions) were identified to enable risks associated specific to urban environments to be distinguished from those associated with other environments.

These geographic coordinate datasets were submitted to BIOSECURE, a GIS-based modelling tool for management of biosecurity risks to New Zealand’s indigenous ecosystems (Barker et al. 2003). The climate module of BIOSECURE is...
Table 1  Details of ant species and number of distribution records used to assess risk to New Zealand.

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Ant species</th>
<th>Current status in New Zealand</th>
<th>Native range</th>
<th>No. of native records</th>
<th>No. of introduced records&lt;sup&gt;a&lt;/sup&gt;</th>
<th>No. of non-urban introduced records</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dolichoderinae</td>
<td>Linepithema humile (Mayr)</td>
<td>Established c. 1990 (Green 1990)</td>
<td>South America (Suarez et al. 2001)</td>
<td>38</td>
<td>417</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>Tapinoma melanocephalum (Fab.)</td>
<td>Interceptions and incursions (S. O’Connor pers. comm. 2006)</td>
<td>Tropical Africa (Fowler et al. 1994)</td>
<td>17</td>
<td>132</td>
<td>117</td>
</tr>
<tr>
<td></td>
<td>Anoplolepis gracilipes (F. Smith)</td>
<td>Interceptions and incursions (S. O’Connor pers. comm. 2006)</td>
<td>Africa? (Shattuck 1999)</td>
<td>2</td>
<td>88</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Tapinoma melanocephalum</td>
<td>Not intercepted (S. O’Connor pers. comm. 2006)</td>
<td>Asia Minor (Seifert 2000)</td>
<td>0</td>
<td>52&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0</td>
</tr>
<tr>
<td>Formicinae</td>
<td>Lasius neglectus Van Loon, Boomsma &amp; András</td>
<td>Interceptions and incursions (S. O’Connor pers. comm. 2006)</td>
<td>Tropical Africa (Fowler et al. 1994)</td>
<td>7</td>
<td>145</td>
<td>132</td>
</tr>
<tr>
<td>Myrmicinae</td>
<td>Monomorium destructor (Jerdon)</td>
<td>Interceptions (S. O’Connor pers. comm. 2006)</td>
<td>Possibly India/SE Asia (Bolton 1987)</td>
<td>16</td>
<td>46</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td>Monomorium destructor (Jerdon)</td>
<td>Established c. 1940 (Harris et al. 2005)</td>
<td>Possibly Africa (Bolton 1987)</td>
<td>20</td>
<td>155</td>
<td>76</td>
</tr>
<tr>
<td></td>
<td>Paratrechina longicornis (Latreille)</td>
<td>Interceptions and incursions (S. O’Connor pers. comm. 2006)</td>
<td>Tropical Africa (Fowler et al. 1994)</td>
<td>23</td>
<td>115</td>
<td>88</td>
</tr>
<tr>
<td></td>
<td>Pheidole megacephala (Fab.)</td>
<td>Established c. 1941 (Berry et al. 1997)</td>
<td>Tropical Africa (Fowler et al. 1994)</td>
<td>137</td>
<td>46</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Solenopsis geminata (Fab.)</td>
<td>Incursions (S. O’Connor pers. comm. 2006)</td>
<td>Tropical Americas (Fowler et al. 1994)</td>
<td>41</td>
<td>693&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>S. invicta Buren</td>
<td>Interceptions and incursions (S. O’Connor pers. comm. 2006)</td>
<td>South America (Taber 2000)</td>
<td>34</td>
<td>22</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>S. richteri Forel</td>
<td>Not intercepted (S. O’Connor pers. comm. 2006)</td>
<td>South America (Taber 2000)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Wasmannia auropunctata (Roger)</td>
<td>Intercepted (S. O’Connor pers. comm. 2006)</td>
<td>Tropical America (Fowler et al. 1994)</td>
<td>102</td>
<td>73</td>
<td>68</td>
</tr>
</tbody>
</table>

<sup>a</sup>For species already established, New Zealand records are not included in the analysis.

<sup>b</sup>All urban records.

<sup>c</sup>For most of the records no specific habitat information was given so the records were not divided into a separate non-urban category.
broadly comparable to the climate match function of CLIMEX (Sutherst & Maywald 1985; Sutherst et al. 1999), but uses climate surfaces rather than data from individual meteorological stations, and extends the comparison of individual sites by extracting climatic data for any given set of point locations, summarising these data, and identifying similar climates globally and across New Zealand (at a finer resolution).

For each location, values for eight climate parameters were estimated from global climate surfaces at half-degree grid square resolution (Appendix 1). The climate surfaces were all derived from thin-plate spline models fitted to 30-year averages for global (New et al. 2000) and New Zealand (Leathwick & Stephens 1998; Rutledge & Wilson 2003) networks of meteorological stations. For each species, a set of realised niche models was fitted, which described the distribution of the species along each of the climatic gradients (Fig. 1). These niche models assumed (from known sampling probabilities) that species are more widespread and abundant (and hence more likely to be detected) in environments close to their realised optimum than elsewhere. Distribution records were assigned to one of 10 equal-width segments that defined that part of the climatic gradient occupied by the species. A smoothed curve was then fitted to data, forced through the x-axis above and below the observed occurrences, to delineate the species realised niche. Based on this niche description, 0.5° grids for the world, and 25 m grids for New Zealand, were allocated risk scores between 0 (outside the range of the species niche) and 100 (maximally occupied segment of the gradient, corresponding to the “optimum” of the species realised niche). For each global grid square a score was allocated for each climate surface.

Data were checked for outliers during fitting of the realised niche models. Individual data points were removed prior to final analyses only if based on a poorly defined location (e.g., presence data without a specific location for a large oceanic islands or regions within a country). Analyses were performed for native and introduced range data separately, and for the introduced range with and without association with urban environments (which included both urban outdoor and indoor records). For presentations that combined native and introduced range records, the risk scores are given as the arithmetic mean of the scores based on separate analyses for native and introduced ranges. In addition to derivation of niche models, the climate envelope of each species was described as the mean and range for each climate parameter.

RESULTS

Temperature is the aspect of climate most likely to limit the New Zealand distribution of 11 of the 12 ant species considered here. This conclusion is based on the general absence in New Zealand of mean annual temperature (MAT) conditions that are typical of the realised niche of these species in their ranges (native and/or introduced) elsewhere. The other aspects of climate considered point to a more general match between observed realised niche and the conditions in New Zealand, and thus predict a level of risk for New Zealand (Appendices 1, 2). *Lasius neglectus* is the one exception to the establishment/distribution pattern predicted for the other species, because the niche defined by MAT from known localities overlaps with most of New Zealand, and the niche defined by rainfall (PREC) is not well represented in New Zealand.

The Kermadec Islands are climatically suitable for most of the species assessed, although temperatures are at the cool end of the realised niches for *T. melanocephalum, M. pharaonis* and *A. gracilipes*, and the climate is possibly too hot and wet for *L. neglectus* (Fig. 2; Appendices 1, 2).

The Chatham Islands are too cold for all except *L. neglectus* and possibly *L. humile* (Fig. 2; Appendices 1, 2). The subantarctic islands administered by New Zealand are largely protected from establishment of invasive ants because their climate is too cold for all species assessed except *L. neglectus*.
The ant species considered in these analyses were divided into four groups in terms of their likely risk to the New Zealand mainland: those with potential to be widespread; species probably restricted to northern distributions; those likely to live only indoors; and those unlikely to establish anywhere.

**Relatively widespread species**

Two of the 11 species were predicted to have widespread distributions in New Zealand, namely *L. humile* and *L. neglectus*. For *L. humile*, large areas of the North Island and the northern South Island, show overlap between the estimated realised niche and predicted niche in New Zealand for MAT (Fig. 2, 3A), although rainfall is likely too high in some areas (Fig. 1A). Three cold outliers from native habitat in Chile (Snelling 1975) were excluded from the dataset. Although *L. humile* is established in Chile (Wild 2004), the excluded records are possibly another species of *Linepithema* (A. Wild pers. comm. 2004).

The estimated realised niche for MAT and mean temperature of the coldest month (MINT) of *L. neglectus* suggest virtually the entire New Zealand mainland is within the predicted niche (Fig. 2, 3B). The estimated MAT of an outlier from Igdir in Turkey (Seifert 2000) is lower than temperatures from any grid square in New Zealand. The estimated realised niche for PREC, which includes a high rainfall outlier in Georgia (Seifert 2000), is low compared with western New Zealand (Fig. 3B).

**Restricted northern distribution**

Climate comparisons indicate *P. megacephala, S. invicta, S. richteri* and *P. longicornis* all have potential to establish outdoors in northern parts of the New Zealand mainland. For *P. megacephala*, the predicted niche in New Zealand for MAT encompasses northern New Zealand (principally due to urban records, from Sana’a in Yemen (Collingwood & Agosti 1996) and an imprecise record from “central Spain” (Collingwood 1978)). The estimated realised niche for MAT from native + introduced non-urban data predicts niche in the northern tip of New Zealand, but this is due to a single record from grassland by a highway in Pietermaritzburg, South Africa (Samways et al. 1997) (Fig. 2, 3C). For MINT, predicted niche in New Zealand is reduced but still encompasses large areas of northern New Zealand.
Fig. 3  Examples of the similarity to New Zealand of mean annual temperature (MAT), mean temperature of the coldest month (MiNT), and annual precipitation (PREC) from the international range of invasive ants. Risk scores between 0 (outside the known range of the distribution records used for the species) and 100 (the climate division with the greatest frequency of data points). A, L. humile (native + introduced non-urban data); B, L. neglectus (all data); and C, P. megacephala (native + introduced non-urban data).
For *S. invicta* and *S. richteri*, the predicted niche indicates overlap with northern New Zealand for MAT (Fig. 2), and within some of this area PREC is above that of the realised niche.

For *P. longicornis*, the predicted niche for MAT includes all New Zealand (Fig. 2) due to records from urban areas within the introduced range (including heated buildings in very cold climates, e.g., Quebec, Francoeur 1977). This species may establish in urban areas, but is unlikely to establish elsewhere as the native + introduced non-urban estimated realised niche for MAT predicts no overlap with the New Zealand mainland.

**Indoor species**
Climate comparisons indicate that *T. melanocephalum, M. destructor, M. pharaonis* and *W. auropunctata* could all establish in New Zealand, but only within heated buildings, as recorded in other temperate climates (e.g., Francoeur 1977; Bolton 1987). However, the estimated realised niche for MAT from native + introduced non-urban distribution records predicts no niche within the New Zealand mainland for *T. melanocephalum* and *M. pharaonis*, and possible overlap with the very northern tip of New Zealand for *M. destructor* (Fig. 2).

For *W. auropunctata*, there is a predicted non-urban niche for MAT in northern New Zealand due to low temperature outliers estimated from the native range. These outliers are from mountainous regions of Colombia (Armbrecht & Ulloa-Chacon 2003) and Ecuador (Wetterer & Porter 2003), but the validity of temperature estimates for these native records are in doubt (see Discussion). Introduced non-urban records for *W. auropunctata* are all from tropical locations and have MAT at least 1.6°C higher than that estimated for the New Zealand mainland (Fig. 2).

**Unlikely to establish**
Climate comparisons indicate New Zealand is too cold for *A. gracilipes*. The estimated realised niche for MAT predicts no suitable niche on the New Zealand mainland (Fig. 2). For *S. geminata*, the MAT from the estimated realised niche indicates that northern New Zealand is just outside the coldest outlier, i.e., a record from Fort Davis in Texas (Moody et al. 1981). However, Moody et al. (1981) consider this record to be dubious due to its separation from other records and the inability of several researchers to confirm its presence. With this record removed there is greater separation between the estimated realised niche and estimated MAT for the northern tip of the New Zealand mainland (Fig. 2).

**DISCUSSION**

**Risks and consequences of ant establishment**
If cool summer temperatures are the primary limiting factor for the species of tropical origin, densities may be higher, and impacts potentially more severe, on the Kermadeces compared to the rest of New Zealand. *Pheidole megacephala*, the only one of the assessed species established on the Kermadeces, is very abundant on Raoul Island (C. Green Department of Conservation pers. comm. 2005) and could be having significant impacts, as it has elsewhere (e.g., Hoffmann et al. 1999).

Climate comparisons indicate that all but two of the species (*A. gracilipes* and *S. geminata*) have some potential to establish in New Zealand. However, when considering MAT, only *L. neglectus* and *L. humile* are predicted to survive outside heated buildings across significant areas, while *P. megacephala, P. longicornis, S. invicta* and *S. richteri* have the potential for limited establishment outdoors in northern New Zealand. MAT in New Zealand is at the low end of the range calculated for all species except *L. neglectus*, and this may limit the presence of all the other species to warmer microclimates and restrict their abundance compared to populations from hotter climates, as appears to be the case for *S. invicta* in cooler northern areas in the United States (Callcott et al. 2000).

*Tapinoma melanocephalum, W. auropunctata, M. destructor* and *P. longicornis* all have the potential to live in suitably heated buildings anywhere in New Zealand, but their distribution is likely to be highly restricted, as is already evident with *M. pharaonis*, which has been detected only sporadically in New Zealand (always in heated buildings) since it was first recorded in the 1940s (Harris et al. 2005). New Zealand is probably too cold for *A. gracilipes* and *S. geminata*, so management of incursions of these species is probably unnecessary. *Anoplolepis gracilipes* does not appear to establish nests indoors in temperate locations. Several records of *S. geminata* from temperate locations exist, but no evidence was found of ongoing establishment, and where nests were reported they were within tropical glass houses (e.g., Ayre 1977). *Anoplolepis gracilipes* and *S. geminata* are established in northern Australia (Young et al. 2001; Hoffmann & O’Connor 2004), but not in southern areas comparable in temperatures to New Zealand.

Climate comparisons indicate that *L. neglectus* has the potential to establish further south than *L. humile*. However, to date *L. neglectus* has been
reported primarily in close association with urban areas (Seifert 2000) so its likely distribution outside of urban areas remains unknown.

Species restricted to heated buildings will have localised impacts, requiring pest management action similar to that already undertaken for the established species infesting buildings (i.e., *Technomyrmex albipes* and *M. pharaonis*). *Paratrechina longicornis* can occupy houses in large numbers in tropical climates (Lee 2002), transport pathogenic microbes in hospitals (Fowler et al. 1993), and alter invertebrate communities in an artificial environment (Wetterer et al. 1999).

The main factor that would significantly alter the pest status of ants in urban environments in New Zealand would be the establishment of species with potent venom. *Solenopsis richteri* and *S. invicta* possess a painful sting capable of causing pustules, and in some cases anaphylaxis and death (Lofgren et al. 1975; Solley et al. 2002). Although the area of New Zealand that has a climate suitable for *S. invicta* and *S. richteri* is relatively small compared with that suitable for *L. humile*, consequences of their establishment may be severe. New Zealand’s most populated city (Auckland), and other coastal cities in the North Island, may be warm enough for *S. invicta* and possibly *S. richteri* (e.g., Auckland, Albert Park MAT (1961–98) = 15.8°C; www.metservice.co.nz (accessed 11 August 2005)). In addition to its sting, *S. invicta* has documented impacts on agriculture and natural systems (Taber 2000).

**Species already in New Zealand**

*Linepithema humile*, *P. megacephala* and *M. pharaonis* are established on the New Zealand mainland. They have very different distributions (Fig. 4), which appear consistent with the climate-based predictions presented here. *Linepithema humile*, first found in Auckland in 1990 (Green 1990), has the widest distribution and is still spreading. Climate comparisons suggest the climate in the upper North Island is most suitable for establishment outside urban areas (Fig. 3A). Future distribution in association with urban areas is predicted to be much wider, and populations have been found as far south as Christchurch (43°53’S).
*Pheidole megacephala*, established since 1942 (Berry et al. 1997), is restricted to a few coastal suburbs of Auckland, is seldom collected, and does not appear to be a pest (Don & Harris 2005). Climate comparisons presented here suggest MAT in northern urban areas is just above the lower range of suitability from the estimated realised niche. Outside urban areas this species is unlikely to flourish, with only the far north of the North Island overlapping with international data (Fig. 3C).

*Monomorium pharaonis* has been collected sporadically from New Zealand since 1941, but only from urban areas, and apart from one sample at the port of Tauranga (which probably represents a recent arrival in the port), always within heated buildings (Harris et al. 2005).

**Climate parameters limiting spread**

For all species other than *L. neglectus*, MAT is the climate parameter for which the range of values from the non-urban realised niche shows the least overlap with New Zealand and was therefore singularly the most useful in predicting risk of establishment in New Zealand. MiNT shows considerably more overlap. This indicates New Zealand summers are generally too cold for these species. There are no explicit experimental data quantifying the likelihood of survival, or the productivity of colonies establishing, at locations with ongoing below average temperatures (e.g., mean annual temperatures in the warmest locations in New Zealand are >1.5°C below any location where *P. longicornis* was recorded in non-urban environments). However, adequate summer temperatures are important to maintain colony productivity, because egg laying, development rates, and foraging activity are all highly temperature dependent (e.g., Porter 1988; Porter & Tschinkel 1993; Korzukhin et al. 2001; Vega & Rust 2001; Palomo et al. 2003), so the assumption is that colonies would not persist. Demonstration of colony decline in suboptimal conditions would allow greater confidence in assessing climate suitability based on temperature limitations.

The temperature of the soil rather than of the air may be the key variable determining the likelihood of establishment, as many of these species typically nest at ground level or just below the surface (Hartley & Lester 2003). Without access to international data on soil temperatures, we used MAT as a surrogate for soil temperature. At the local scale, vegetation and litter cover will influence soil temperature and ability to colonise forest (Ward & Harris 2005).

*Lasius neglectus* is adapted to temperate climates, so New Zealand temperatures are less likely to restrict its distribution than is high rainfall. However, *L. neglectus* is a relatively newly discovered pest (Van Loon et al. 1990); virtually nothing is known about its native range (Seifert 2000), and it is still spreading into new areas (Seifert 2000). Therefore, it may still spread into higher rainfall areas, which would greatly increase the extent of the predicted areas of establishment in New Zealand.

**Risk of establishment in the Pacific**

Most other countries in the Pacific have warmer climates than New Zealand, and therefore are more suitable for all of the tropical species (e.g., MAT over much of Australia is within the estimated niche of *P. megacephala*; Fig. 5), and most of the assessed species are already widely distributed throughout the Pacific. Patterns of high and low rainfall may have greater influence on the local distribution of species in these areas.

**Limitations of approach**

The approach taken to assess the risk of these species is relatively simple, and the data are coarse. Such a simplistic approach is necessary where there is limited information on climatic preferences—which is the case for most of the ants assessed here—and where global records of limited precision are available. The aim is not to be able to predict presence or absence at any specific location with a high degree of certainty, but to provide a general indication of spatial pattern and degree of likely risk to New Zealand. Pearson et al. (2006) demonstrated that the use of alternate modelling approaches produced quite different predictions of species range, so predictions made from them should be treated with caution. Predictions of methods using presence/absence data were distinct from those using presence only, but it was difficult to single out a “best” technique (Pearson et al. 2006). They concluded that there needs to be a high degree of interpretation of results in risk assessment and full appreciation of uncertainty inherent in such techniques rather than unquestioned acceptance of predictions. Clearly in order to increase confidence in the inability of potential pest species to establish (such as *S. geminata* and *A. gracilipes*), assessment by several alternate methods would be advisable.

The global climate data used here are based on 0.5° grid squares, and while higher resolution data are becoming available (e.g., 1 km resolution), their use in this risk assessment context may not result
in greater precision of assessments, primarily because many of the distribution records on which the analyses are based are themselves imprecise. Errors associated with spatial inaccuracies of locality data can result in substantive errors in estimates of climate parameters for landscapes that have more fine-scale heterogeneity than those on which the climate surfaces are based. For example, if an ant location record is in a valley within an otherwise mountainous region, the temperature at the actual location occupied by the ant is likely to be higher than that estimated for that 0.5° grid square. This type of error probably explains the MAT cold outliers from South America in the *W. auropunctata* analysis (although Lester (2005) predicts establishment risk for this species in New Zealand) and a cold outlier for South Africa in the *P. megacephala* analysis. An alternate method to eliminate outliers would have been to use trimmed ranges (e.g., central 95%). In the case of *W. auropunctata*, the climate envelope for MAT would then become 16.2–25.7°C, i.e., with considerable less overlap with New Zealand than predicted. However, we chose to adopt the precautionary principle and include all submitted data in the analysis, and exclude specific outliers only when manual inspection of the data showed there was appropriate justification. This approach allowed us to highlight where there is doubt and a need to further clarify risk.

Within any area there will be microhabitats that differ from the surrounding habitat. An ant may be present in a particular microclimate but otherwise absent from the surrounds. In such cases, risk assessment tools such as BIOSECURE will underestimate risk for landscapes where suitable microhabitat might be confined to spatial scales insufficient to alter the macroclimate on which climate surfaces are based.

No analysis of interactions between climatic gradients has been attempted. Apart from temperature and rainfall, which clearly restrict ant species distributions (e.g., Ward 1987; Korzukhin et al. 2001), it is not known if the extremes of the other climate parameters (outside values from a species current range) would actually limit a species, and their inclusion in the risk analysis can give spurious areas of high risk. For the ants assessed here, consideration of mean annual temperature and rainfall is sufficient to indicate risk. However, where temperature and rainfall parameters are near their lower limits for a species, the chances of successful establishment are probably lowered. In the case of *L. humile*,

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**Fig. 5** Example of the global similarity of MAT values of native + introduced non-urban data of *P. megacephala*. Risk scores between 0 (outside the known range of the distribution records used for the species) and 100 (the climate division with the greatest frequency).
interactions between temperature and rainfall suggest that temperature optima increase as precipitation increases (Hartley et al. 2006).

If there are limited data on species distribution, the climate envelope is likely to be underestimated, potentially leading to an underestimation of potential niche. Also the assumption in the niche models, that optimum climate corresponds to that with the most distribution data, will not always be correct, resulting in a distortion of the zones of highest risk, if greater sampling effort for many species correlates with areas of higher human population.

Factors other than climate can limit distribution, particularly in the native range. For example, *S. invicta* occupies a broader climatic range where it has been introduced into North America than it does within its native range (Fitzpatrick et al. 2007). In South America interactions with other ant species (first speculated on by Bure et al. 1974), including a diverse *Solenopsis* fauna (Trager 1991), and the impact of parasitoids (Folgarait & Gilbert 1999), may contribute to their more restricted distributions. However, it could be that a wider climate tolerance is revealed by more records, as species with more data for their native range (e.g., *S. geminata* and *W. auropunctata*) do not show a reduced climate envelope in their native range compared to the introduced range. For 19 of the 28 adventive ants established in New Zealand, there are no other records of establishment outside their native range. An *a posteriori* consideration of the risk to New Zealand of some of the 19 species with only native range data would indicate the applicability of climate comparisons for assessing the risk of species that have not spread beyond their native range.

**Comparisons to other approaches**

Other studies have focused on detailed assessments of the suitability of New Zealand for single species of ants, and used a subset of the data to create test and training datasets. Although the approach is different in each study they show results broadly similar to ours: New Zealand is too cold for *A. gracilipes* (Lester 2005), marginal for *S. invicta* in northern New Zealand (Morrison et al. 2004; Lester 2005; Sutherst & Maywald 2005), and suitable for *L. humile*, particularly in the North Island (Harris 2002; Hartley & Lester 2003; Hartley et al. 2006). A soil-based temperature model predicted several southerly locations suitable for *L. humile* that were considered too cold when based on air temperature (Hartley & Lester 2003).

An alternate risk assessment compared the climate of New Zealand’s main entry point for invasive species, the city of Auckland, to the climate from meteorological stations around the world (Peacock & Worner 2006). Areas of high similarity corresponded to areas where *L. humile* (e.g., the Montevideo (Uruguay), Porto Alegre (Brazil) region of South America) and *L. neglectus* (western Europe) are widely distributed, and the northern distribution of *S. invicta* and *S. richteri* (the east coast of the United States), Peacock & Worner’s (2006) areas of high climate similarity show little overlap with the distributions of the other ant species we assessed. The usefulness of all these models is the general patterns of national or global predicted niche and comparisons of optimal climate between species.

Many ant species survive in urban areas below their lower temperature limits because of warmer microhabitats. For example, *M. pharaonis* is found nesting and foraging outdoors in tropical environments but lives exclusively indoors in temperate regions such as Europe (Passera 1994). For many distribution records in the scientific literature it is difficult to determine from the information presented if the collection site is an urban habitat or elsewhere. Within urban areas it is often unclear if the species survives exclusively outdoors or uses thermoregulated habitats. If urban records are included in an analysis it is likely to overestimate temperature tolerances and the risk to native habitats in New Zealand.

**Climate change**

With the exception of *L. neglectus*, the risk of establishment in New Zealand is limited principally by temperature. MAT data are based on long-term averages. Above average years may allow species to establish that are otherwise not predicted to establish. In cooler years such species may disappear or they may survive in refuges with elevated temperatures. With predicted global warming, temperatures may remain elevated long term. Some scenarios for changes to New Zealand’s temperatures over 100 years suggest by 2080 summer temperatures in the North Island could be 2°C warmer than now (Mullan et al. 2002). At these elevated temperatures the risk of establishment of some of the invasive species would increase, with the lowest records from non-urban habitat showing some overlap with New Zealand (e.g., *S. geminata*; Fig. 6). The range within New Zealand for established species would likely increase, and species that are currently not pests,
P. megacephala for example, might become so. Rainfall patterns are predicted to remain similar in the northern half of the North Island, but over the rest of New Zealand to increase in the west and decrease in the east (Mullan et al. 2002), which might alter the distribution of some species.

Management of incursions
Our predictions, supported by other climatic studies, indicate that the chances of temporary establishment of colonies of species such as S. geminata and A. gracilipes can be ignored, as temperatures in New Zealand are below those encountered anywhere else they survive. Obviously the cost, both financial and environmental of an incorrect prediction for a well documented pest species is high, and precaution is probably the best policy. However, for many other tropical species, without documented impacts, the consequences of an incorrect assessment would be minimal.

Ideally, biosecurity authorities want to test the validity of climatic predictions and of estimated biological responses of species to suboptimal climate. Pheidole megacephala, a species with a very restricted range in New Zealand, provides the ideal opportunity to test the effects of suboptimal climate. This could be done through assessment of nest density and productivity in its current location compared to predicted optimal and marginal habitat in Australia, accompanied by a study of the productivity of colonies relocated along a climate gradient.

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New Zealand Journal of Zoology, 2007, Vol. 34


Taber SW 2000. Fire ants. Texas, College Station, Texas A&M University Press.


Appendix 1  Climate parameters used in BIOSECURE and summary data (mean and range) for the globe and New Zealand from 0.5° global climate surfaces.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Code</th>
<th>Global range (excluding Antarctic continent)</th>
<th>Kermadec Islands</th>
<th>New Zealand mainland (North, South and Stewart Islands and surrounding small offshore islands)</th>
<th>Chatham Islands</th>
<th>Subantarctic Islands (Antipodes, Auckland, Bounty, Campbell)</th>
</tr>
</thead>
<tbody>
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<td>196</td>
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<td>8</td>
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<td>MAT</td>
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<td>10.9</td>
<td>11.7</td>
<td>7.8</td>
</tr>
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<td>2.2</td>
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<td>MAT_S</td>
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<td>8.8</td>
<td>7.3</td>
<td>6.5</td>
</tr>
<tr>
<td>Annual precipitation (mm)</td>
<td>PREC</td>
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<td>1394</td>
<td>1765</td>
<td>886</td>
<td>1118</td>
</tr>
<tr>
<td>Seasonality of precipitation—absolute difference in mean precipitation between the wettest and driest months (mm)</td>
<td>PREC_S</td>
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<td>67</td>
<td>60</td>
<td>46</td>
<td>36</td>
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<td>Annual mean of the monthly mean vapour pressure (kPa)</td>
<td>VP</td>
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<td>18.3</td>
<td>9.7</td>
<td>11.0</td>
<td>8.3</td>
</tr>
<tr>
<td>Seasonality of vapour pressure—absolute differences in mean vapour pressure between the most humid and the least humid months (kPa)</td>
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<td>5.9</td>
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<td>3.4</td>
</tr>
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<td>Annual mean of monthly mean solar radiation (MJ/m²/day)</td>
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**Appendix 2**  Summary of the climate envelopes derived from the distribution records of each ant species (excluding New Zealand). The mean of each parameter from the input data and the range is presented. The data are grouped into native (N), introduced (I), and the introduced non-urban records (I (nu)).

<table>
<thead>
<tr>
<th>Species</th>
<th>Group</th>
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<th>MINT</th>
<th>MAT_S</th>
<th>PREC</th>
<th>PREC_S</th>
<th>VP</th>
<th>VP_S</th>
<th>MAS</th>
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<td>mean</td>
<td>mean</td>
<td>mean</td>
<td>mean</td>
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<td>100.2</td>
<td>15.6</td>
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</tr>
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<td>8.4</td>
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<td>(0–343)</td>
<td>(5–28)</td>
<td>(2–19)</td>
<td>(10.8–20.7)</td>
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</tr>
<tr>
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<td>(6–24)</td>
<td>(4–18)</td>
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<td>(5–670)</td>
<td>(7–31)</td>
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</tr>
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<td>(1–17)</td>
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Appendix 2 (continued)