

## The potential distribution of German wasps (*Vespula germanica*) in Argentina

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**Abstract** In the early 1980s, the German wasp (*Vespula germanica*) arrived in Argentina and became established in northern Patagonia. We use an ecoclimatic computer-based program (CLIMEX) to predict the potential spread of wasps to other areas of the country. The model suggests that much of Argentina does not appear to be very suitable for the species' establishment. However, more suitable areas than those currently colonised by the wasp occur in the centre of the country. Based on CLIMEX results, we suggest that, if the wasps ever break through the barrier of unfavourable habitat that surrounds their current distribution, they will continue dispersing to those areas. Notwithstanding this, factors other than climate may explain why German wasps are firmly established in areas otherwise considered to be inhospitable for the species.

**Keywords** social insects; Patagonia; biological invasions; ecoclimatic matching

### INTRODUCTION

Several species of ants, wasps, and bees have proved to be highly successful invaders of new territories, often becoming pests by causing damage to crops, increasing medical expense, or by disrupting outdoor activities (Moller 1996). As with most biological invasions, the spread and establishment of these social insects in a new habitat depends on several ecological factors such as the attributes of the receiving community and the invader's own characteristics (Lodge 1993). Although several physical and biological factors affect a species' potential distribution, it has long been suggested that the ultimate limits to the distribution of most poikilothermic animals are determined by climate (Andrewartha & Birch 1954). Thus, successful establishment of an invader depends on an adequate ecoclimatic matching between the invading species and the invaded system (Crawley 1986).

The German wasp (*Vespula germanica* Fab.) is native to Eurasia and Northern Africa, thus having a wide geographical range there (Archer 1998). It has also become established in New Zealand (Thomas 1960), Australia (Spradbery 1973), South Africa (Tribe & Richardson 1994), North America and Canada (MacDonald et al. 1980), and Chile (Edwards 1976). Because wasps in high numbers damage economic activities and natural ecosystems, such as beekeeping, horticulture, tourism, and cattle rearing, there has been extensive research on controlling *Vespula* populations in colonised areas (Akre & MacDonald 1986; Barlow et al. 1996; Beggs et al. 1998; Beggs 2001; Harris & Etheridge 2001; Sackmann et al. 2001). In addition, the painful (rarely fatal) sting may interfere with human outdoor activities and affect residential areas where wasps are attracted to stored food and rubbish (Akre & MacDonald 1986).

In the early 1980s, a few individuals of the German wasp were observed in the Neuquén province, Argentina (Willink 1980), which had probably arrived from Chile through the low mountain passes near Chos Malal. Since then, the

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species has dispersed rapidly through Patagonia (Willink 1980) but has not been reported yet in other areas of the country (see Fig. 1; Corley et al. 1997; Sackmann et al. 2000a). As in other regions of the world where it has invaded, this wasp behaves as a pest almost throughout its distribution range where it also preys upon native arthropod species (Sackmann et al. 2000b).

It has been suggested that climate is not only one of the main factors that determines the distribution of German wasps but is also an important element in determining invasion success (Kemper 1960; Edwards 1976; Madden 1981). The German wasp is successful under cool to very hot conditions, but is sensitive to prolonged cold as well as hot conditions (Spradbery & Maywald 1992). Some studies have shown that rainfall plays a major role in regulating social vespine populations. Madden (1981) and Horwood et al. (1993) found a positive correlation between nest numbers of German wasps and rainfall in Tasmania and New South Wales (Australia). In turn, others have suggested that rainfall, together with low temperatures, suppress *V. vulgaris* and *V. pensylvanica* numbers by flooding under-

ground nests, or by destroying newly established colonies (Fox-Wilson 1946; Akre & Reed 1981).

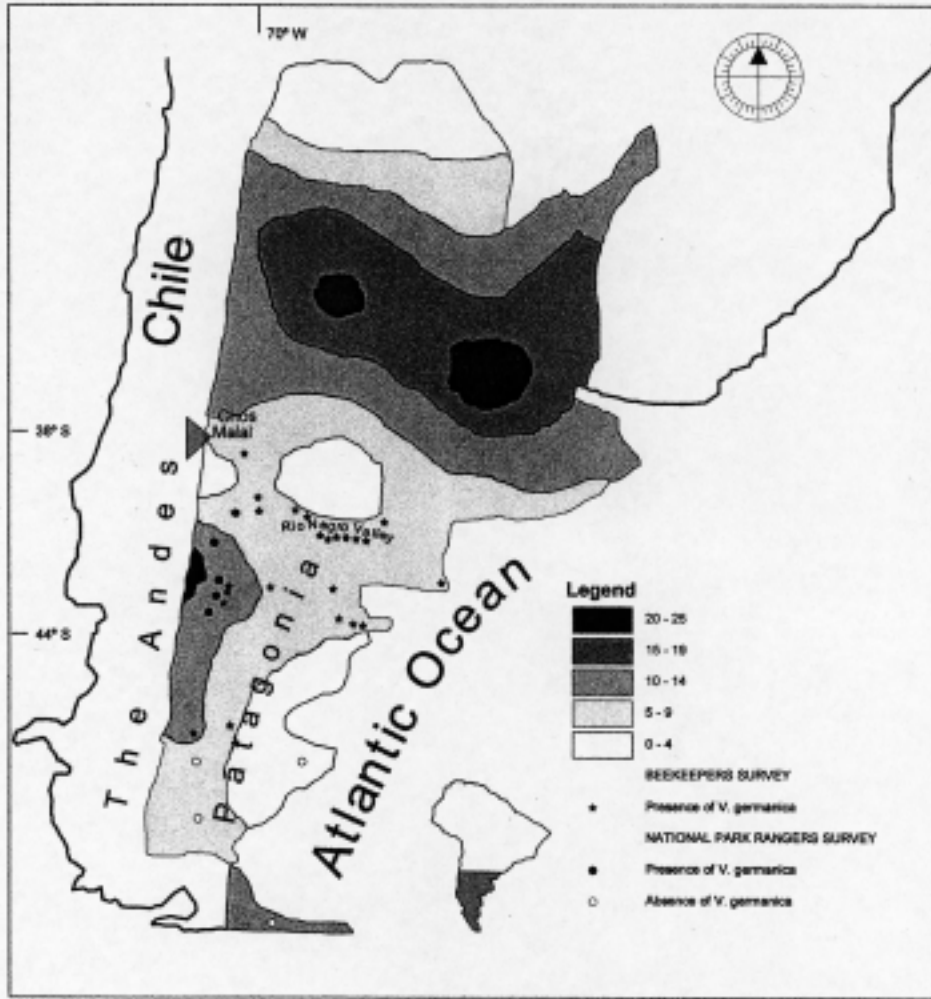
To predict the potential distribution of German wasps in Argentina, we compare the climate in its original distribution range with the climatic conditions found in Argentina by means of ecoclimatic matching techniques (Spradbery & Maywald 1992; Tribe & Richardson 1994; Williamson 1996). By comparing these results with the current distribution of the German wasps, we can deduce the importance of other ecological features of the species (and of the invaded region) in understanding its successful invasiveness.

## METHODS

CLIMEX (CSIRO CX 18183A; Sutherst et al. 1999) is a simple computer program that predicts the potential distribution and abundance of a species in a new area from climatic and biological data and the known geographic distribution of that species. CLIMEX works on the assumption that the distribution of a species is solely determined by

**Table 1** Values of the physiological parameters of the German wasp by CLIMEX (Spradbery & Maywald 1992).

	<b>Moisture parameters</b>	
SM0	Limiting low soil moisture	0.0
SM1	Lower optimal soil moisture	0.6
SM2	Upper optimal soil moisture	1.5
SM3	Limiting high soil moisture	2.5
	<b>Temperature parameters</b>	
DV0	Limiting low temperature	10.0°C
DV1	Lower optimal temperature	18.0°C
DV2	Upper optimal temperature	26.0°C
Dv3	Limiting high temperature	33.0°C
PDD	Minimum day-degrees	350.0
	<b>Stress indices</b>	
DTCS	Cold stress day-degree threshold	10.0
DHCS	Cold stress day-degree rate	0.00014
TTHS	Heat stress temperature threshold	31.0°C
THHS	Heat stress temperature rate	0.0035
SMDS	Dry stress soil moisture threshold	0.2
HDS	Dry stress rate	0.006
SMHS	Wet stress soil moisture threshold	2.5
HWS	Wet stress rate	0.002
TTHW	Hot-wet temperature threshold	26.0°C
MTHW	Hot-wet moisture threshold	0.8
PHW	Hot-wet stress rate	0.03



**Fig. 1** Environmental suitability of Argentina for the establishment of German wasps (*V. germanica*). Areas with given ecoclimatic indices (EI) values are shown with different shades of grey, ranging from unsuitable (EI of 0–4, white) to favourable (EI of 20–25, black). For details of how the isoecoclimatic map was generated from 159 localities, see text. Data from two surveys, documenting the presence/absence of wasps in nine national parks and 23 other localities are also shown. The probable site where wasps first arrived in Argentina is shown by a triangle.

climate. It also assumes that most animal and plant populations experience a season that is favourable for population growth, and an unfavourable one that may jeopardise the species' persistence at a given location. The program compares ecoclimatic indices from the known distribution range of the species with those of other areas (e.g., where the species has been introduced). It derives an ecoclimatic index (EI) from the physiological parameters of the species and from meteorological data, which describes the suitability of a given location for the species under

study. Each local EI integrates the annual growth index ( $GI_A$ ), which describes the potential for population growth, with the annual stresses that are assumed to limit survival during the unfavourable season. The EI is scaled from 0 (unsuitable) to 100 (optimum). An EI close to 0 indicates that a site is not favourable for the long-term survival of the species. EI values of 100 are achievable only under constant and ideal conditions. An EI greater than 30 represents a very favourable climate for a species, because it means that during the (for example) 6

months suitable for growth with a maximum  $GI_A$  of 50, a species with a local EI of 30 has achieved 60% of its potential of population growth on the assumption that there was no stress.

The EI is computed as follows:

$$EI = GI_A \times SI \times SX$$

given that the annual growth index

$$(GI_A) = \frac{100 \sum_{i=1}^{52} GI_{Wt}}{152},$$

the annual stress index ( $SI$ ) =  $(I - CS/100) (I - DS/100) (I - HS/100) (I - WS/100)$ , and the stress interaction index ( $SX$ ) =  $(I - CDX/100) (I - CWX/100) \times (I - HDX/100) (I - HWX/100)$ .

Where  $GI_W$  describes the weekly suitability of the climate for the growth of (for example) a population of insects; CS, DS, HS, WS, are the annual cold, dry, hot, and wet stress indices respectively, and CDX, CWX, HDX, and HWX are the annual cold-dry, cold-wet, hot-dry and hot-wet stress interaction indices (Sutherst et al. 1999).

The parameter values for German wasps incorporated in CLIMEX (Table 1) were estimated using the known distribution of the wasp in Europe, Asia, the Middle East, and Northern Africa (Spradbery & Maywald 1992). We assume that the physiological parameters of these populations are not substantially different from those of the local populations, since they established only 20 years ago. Climatic variables include long-term monthly averages of rainfall and temperature (average minimum and maximum), in addition to latitude, longitude, and altitude. Climatic data for 159 localities in Argentina were obtained from the *Instituto Nacional de Tecnología Agropecuaria* meteorological stations.

We created an isoclimatic map to estimate the location of most and least favourable areas for *V. germanica* establishment in Argentina. First, EIs for each of the 159 localities were located onto a cylindrical equal area projection (i.e., Peter's projection; Peters 1989) of South America, overlaid by a grid of 170 cells, each one covering approximately 123 000 km<sup>2</sup> in reality. Second, contour lines linking cells of equal EIs were obtained by the application of a geostatistical technique that uses an estimation of the semi-variance of the data to perform interpolation ("kriging", see Matheron 1963; Rossi et al. 1992).

Onto the isoclimatic map, we overlapped data on the current distribution of the German wasp in Argentina. These data were obtained through

systematic surveys conducted among national parks rangers and beekeepers (Corley et al. 1997; Sackmann et al. 2000a).

## RESULTS

The isoclimatic map for the German wasp in Argentina is shown in Fig. 1. This map also documents the current distribution of wasps in the nine national parks of southern Argentina and in other localities in the country. Much of Argentina does not appear to be suitable for the establishment of this species. The most favourable areas have an average EI of 20–25, but they are small compared with the total surface area of the country. These sites are considered to have a Mediterranean climate, which is highly favourable for the species. However, no wasps have been recorded in any of them yet. Areas with an average EI of 10–15 offer marginal conditions for the establishment of the wasp. However, German wasps are presently established in north-west Patagonia (which has an EI of 10–15) between 38–44°S (Fig. 1). An inhospitable area surrounds north-west Patagonia which has an average EI of 0–10. The German wasp is also present in one of these areas (which has an average EI of 5–10) but is limited to an artificially irrigated flood plain of the Río Negro valley. The Patagonian coast and the north of the country are predicted to be inhospitable for the establishment of German wasps.

## DISCUSSION

According to the ecoclimatic model CLIMEX, most of Argentina is unsuitable for the establishment of German wasps. The EIs for southern Argentina, where the German wasp is established, are lower than those calculated for areas in other countries which have been successfully invaded by this species. In South Africa, for instance, the German wasp is confined to areas with an average EI of 40 (Tribe & Richardson 1994). Australia also has higher EIs in the south-eastern coast than those found in Argentina (Spradbery & Maywald 1992). A similar pattern is observed in New Zealand, especially in the North Island which has the highest densities of the German wasps and an average EI of 43 (data extracted from CLIMEX).

In Argentina, at present, the German wasp is established in areas where the average EI is around 10–15. Estimations of the density of German wasp

populations in north-west Patagonia beech forests are three to eight times lower than those recorded in comparable New Zealand localities (Sackmann et al. 2001). Notwithstanding this, the species is regarded as a pest of several human activities and for the native arthropod populations, suggesting that they do not need to reach high population densities to pass a damage threshold (Sackmann et al. 2001). High densities of wasps have been recorded in New Zealand and Tasmania at localities with EIs of 11–55 and 24 (Tribe & Richardson 1994). Therefore, according to the model's prediction, wasps may still reach higher densities than those now observed in Patagonia, and if they manage to spread to more suitable areas (i.e., with EIs of 20–25), they may establish even larger populations. On the other hand, considering the low average EIs for Argentina, wasp populations in this country might not reach the high levels found in other parts of the world.

Because German wasps are still dispersing in Argentina, the absence of wasps in some regions might be related to historical rather than ecological events. According to CLIMEX, new populations of the wasp should be expected to occur at the centre of the country where there are areas that appear to be favourable (EI of 15–20 or 20–25) for wasp establishment. There is an inhospitable band separating these areas from the region currently occupied by wasps, which might be limiting their spread. But, it is unlikely that this area will remain a barrier for German wasp dispersal, given their synanthropic behaviour. The southern tip of the country has an average EI similar to that of the region presently inhabited by the wasps (EI of 10–15), which suggests they could also become established in this area.

Although climate is a major factor in determining the distribution of species, there are obvious discrepancies between the predicted and current distribution of German wasps in Argentina. There are ecological factors other than climate that have to be taken into account (Farji-Brener & Corley 1998). German wasps behave in ways that may aid the species in surviving or establishing in ecoclimatically inhospitable areas (Spradbery & Maywald 1992). Inseminated queens search for well-insulated places in which to hibernate, a feature that can have important consequences on wasp dispersal. Queen hibernation behaviour has meant their survival in cargo to distant parts of the world (Spradbery & Maywald 1992). Also, as German wasps are social insects, they have foraging behaviours that can increase the

effectiveness of resource exploitation (D'Adamo et al. 2000).

Furthermore, human activities may change the environment fundamentally, for example through irrigation. The valley of the Río Negro is an area with an average EI of 5–10, where wasps are present. Fruit production is a major activity in this area, so food resources and water are unexpectedly plentiful for wasps. In addition, German wasp often take advantage of buildings to make their nests (Akre & MacDonald 1986). Finally, other factors that may have favoured German wasp establishment are the absence of the parasites, predators, and pathogens that impact on the wasp in its endemic range (Spradbery 1973; Farji-Brener & Corley 1998) and of competition from resident *Vespula* or *Vespa* (hornet) species (Matsuura 1984; Spradbery 1991), which are not present in Argentina.

We conclude that Argentina, although not climatically ideal for the establishment of German wasps, could support more widespread and damaging populations than it does now. On the one hand, human disturbance and mobility might be central events promoting successful wasp invasion. On the other hand, the reported high plasticity of this species, evidenced by its tolerance to a wide range of physical conditions, its social foraging behaviour coupled with its ability to shift diets according to resource availability, and its flexible nesting habits, may be important features which help explain the remarkable invasion success of this species.

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