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PREDICTING ARGENTINE ANT INVASION ACROSS SPATIAL SCALES VIA ECOLOGICAL NICHE MODELS

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Declaration

I hereby declare that the present thesis has been fully worked out by myself and the named co-authors, which allow me to publish our work as a part of my PhD thesis

Núria Roura-Pascual

Girona, December 2006

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A la meva família, i a totes les formiguetes

En un formiguer es formigueja molt.
És un bullit de formigues que van i vénen,
entren i surten, furguen i trajinen,
remenen i belluguen…, sense parar mai.

E. Teixidor
(*La Formiga Piga es deslloriga*)

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General introduction

Global change and biological invasions

Biological invasions happen when species are transported to new geographic areas, where their descendants proliferate, spread, and persist (Elton (1958) in Mack et al. (2000)). In fact, biotic invasions are the last step in a multistage process (Figure 1) that requires the species to overcome various abiotic and biotic barriers (Williamson 1997).

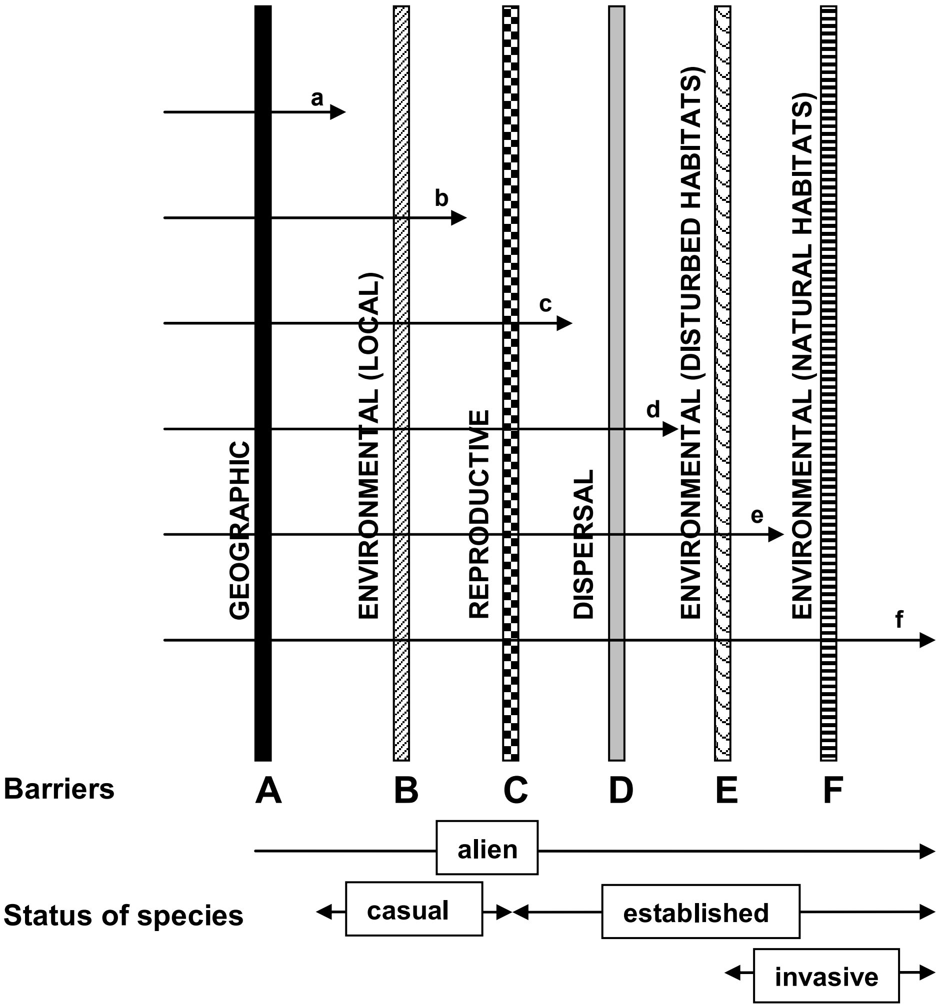

Figure 1 Diagram of major barriers limiting the spread of introduced species (adapted from Richardson et al. (2000), and slightly modified by McNeely et al. (2001)). See page 16 for a full explanation of each barrier. Arrows **a** to **f** indicate the status of the species in the non-native area, referring 'c' and 'd' to non invasive established and 'e' and 'f ' to established but invasive species.

According to Richardson et al. (2000), the starting point of an invasion implies the arrival of an *alien*[1] species somewhere beyond its native range, which supposes the overcoming of the first major geographical barrier (Figure 1-**A**). Once introduced, many species (called *casual*) fail to maintain their populations over long periods without relying on successive introductions for their persistence. The establishment starts when environmental conditions at the site of introduction (Figure 1-**B**) and reproductive success (Figure 1-**C**) allow the survival of the species. An alien species is thus considered successfully *established*[2] when it is able to sustain a viable population without human intervention. Then, if they are able to overcome barriers to dispersal (Figure 1-**D**), species spread into areas close to the introduction site. However, established species are only considered *invasive* when they successfully face abiotic and biotic environmental conditions, and have the potential to spread over extensive areas far away from the introduction site. Many species usually invade human-disturbed habitats or habitats dominated by alien species (Figure 1-**E**), but others are also able to spread through natural or seminatural habitats (Figure 1-**F**) (Richardson et al. 2000, McNeely et al. 2001). Species invasion can thus be summarized as a complex phenomenon which includes introduction and establishment of non-native populations, the ecological appropriateness of new areas, and further spread across these areas (Peterson 2003).

Invasions are not novel events, but the number of species that has been introduced both accidentally or deliberately into new ranges has increased exponentially over the last 500 years, and especially in the past 200 years due to the increase in human transport and commerce worldwide (di Castri 1989). As a result, biotic invasions are recognized to constitute not only a consequence but also a significant component of human-driven global change (Vitousek et al. 1996, Sala et al. 2000, Hulme 2003). According to Vitousek et al. (1997)'s perspective of global environmental change (summarized in Figure 2), biotic invasions are a third level consequence of global change, which in turn is responsible for the Earth's biodiversity losses. Invasions affect biological diversity by changing native species communities and disrupting ecological processes in ecosystems (Vitousek et al. 1997, Chapin et al. 2000, Sala et al. 2000, Olden et al. 2004), which have severe economic repercussions mainly due to losses in potential economic outputs, direct costs of combating the invasion, and affectations to human health by agents or vectors of certain diseases (Mack et al. 2000, Pimentel 2002). However, the agent responsible for the increase in biological invasions and their negative impacts is the movement of humans and merchandises worldwide, ultimately caused by the explosive growth of human populations and per capita use of resources over the last few centuries.

Both deliberate and accidental introductions of non-native species by humans varies among taxonomic groups (Vitousek et al. 1997), and insect fauna have the potential to spread easily over long distances (Simberloff 1989, Lawton 1995). Among the world's worst invasive species (http://www.issg.org/database/welcome/) there are several ant species (McGlynn 1999) which produce highly negative impacts on habitats or ecosystems far away from their native ranges (Williams 1994, Holway et al. 2002a).

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[1] Other synonyms of alien species used indistinctly in this PhD thesis are: exotic, non-native, and nonindigenous species.

[2] At this stage of the biotic invasion process, Richardson et al. (2000) suggested using the term *naturalized* species. However, I preferred to use the term established species, as did by McNeely et al. (2001), for all invasive species rather than only plants.

*Argentine ant (*Linepithema humile *Mayr)*

One of these widespread invasive ants is the Argentine ant (*Linepithema humile* Mayr, formerly called *Iridomyrmex humilis*), from the Dolichoderinae subfamily (Figure 3). Workers of this ant are small dark brown ants of 2-3 mm in length, displaying extremely fast movements and recruiting in high numbers (Newell and Barber 1913). The native distribution of the Argentine ant seems to be the Paraná River drainage basin in subtropical South America (between northern Argentina, southern Brazil, Uruguay, and Paraguay), but it is now established in many Mediterranean and subtropical areas around the world (Suarez et al. 2001, Tsutsui and Suarez 2003, Wild 2004). Dispersion proceeds via two main processes: diffusion dispersal through budding, and long-distance jump dispersion through human-mediated transport (Suarez et al. 2001). In contrast to the usual strategy of colony reproduction in ant species, in which winged sexuals experience nuptial flights and newly mated queens found new colonies independently of and far away from their natal sites, queens of Argentine ant do not undergo mating flights (Hölldobler and Wilson 1990). New colonies are only formed by budding, when inseminated queens leave their nests on foot accompanied by a group of workers to form a new colony in their vicinities (Bourke and Franks 1995). Studies monitoring Argentine ant invasion fronts reported rates of spread between 0 and 300 m/yr (Suarez et al. 2001), and evidenced both seasonal and year-to-year fluctuations in the invasion pattern (Casellas 2004, Heller et al. 2006). Given these limited dispersal capacities, the role of long-distance jump-dispersion is therefore crucial to understand the spread of the species at broader spatial scales: Argentine ants have been introduced in many areas around the world through human transportation and commerce, and subsequent jump-dispersal events from these

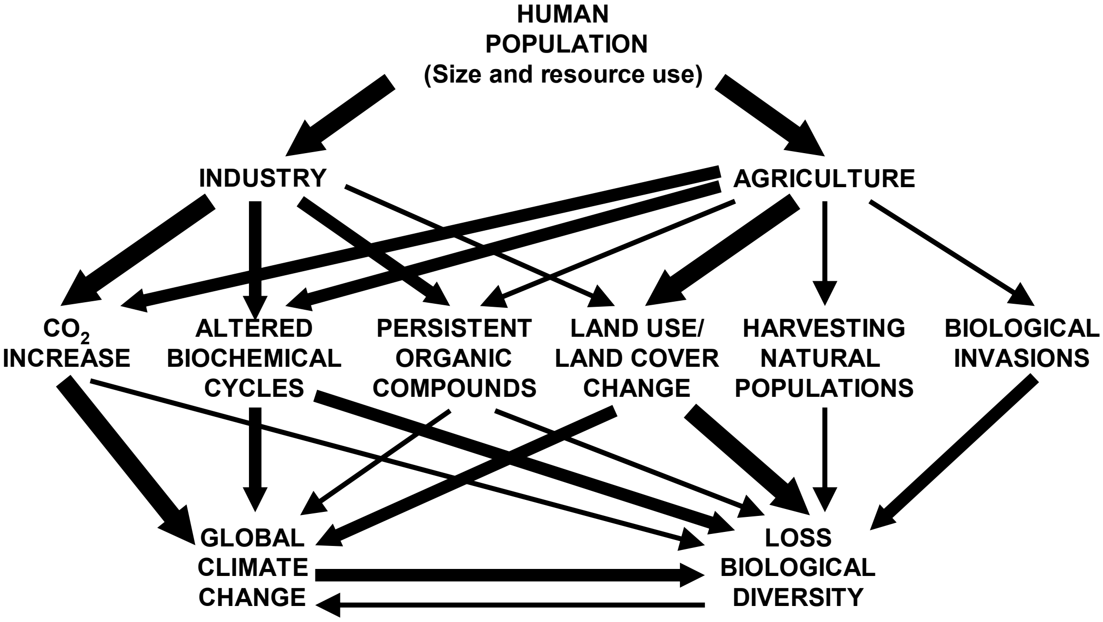

Figure 2 Representation of the main components of the human-induced global environmental change (adapted from Vitousek et al. (1997)). The explosive growth of human populations and per capita use of resources (first level) have supposed an increase in industrial and agricultural-related activities (second level), which cause a set of global environmental changes (third level). These six human-caused changes in turn are responsible for the present-day global change and major losses of biological diversity (fourth level).

original introduction sites would have expanded the invasion into neighboring sites tending to cluster at landscape scales (Suarez et al. 2001). Once established in new areas, Argentine ants spread through a diffusion-like manner into contiguous habitats. However, since jump-dispersal events may occur from few to thousand kilometers, the distance and rate at which such events occur may be more important at broad spatial scales than the spread through diffusion from already invaded areas (Suarez et al. 2001).

Like other invasive species, in addition to its anthropophilic tendency (Passera 1994) and its opportunistic requirements for propagule success (Hee et al. 2000), multiple factors have been associated with the ability of the Argentine ant in invading areas all over the world. The capacity to tolerate a wide range of abiotic conditions (Human et al. 1998, Holway et al. 2002b) and the generalist dietary requirements (Markin 1970) allow the species to easily spread and occupy a broad range of ecological niches. Some studies also indicated changes in social behavior and colony genetic structure as being responsible for the success of *L. humile* (Tsutsui and Suarez 2003, Buczkowski et al. 2004, Holway and Suarez 2004). These studies reported that, in contrast to the native area, Argentine ants are highly unicolonial throughout their introduced range, forming large supercolonies of multiple interconnected nests within which intraspecific aggression is almost absent among individuals from different nests (Suarez et al. 1999, Tsutsui et al. 2000, 2001, Giraud et al. 2002). However, recent findings on the social organization of Argentine ants questioned the existence of such differences among native and introduced populations (Jaquiery et al. 2005). Contrary to the assumption that native populations consist of family-based colonies who are aggressive towards members of other colonies, Pedersen et al. (2006) revealed that: both native and introduced populations of Argentine ants are organized in supercolonies of unrelated individuals, and the only difference is that supercolonies are several orders of magnitude smaller in the native range (25-500m). Hence, the success of *L. humile* invasion does not seem due to changes in social organization after introduction, but to large dimensions of supercolonies in the introduced range. Anyway,

Figure 3 Argentine ant (*Linepithema humile* Mayr) tending scale insects on citrus trees in California (with A.L. Wild permission, extracted from http://www.myrmecos.net/)

this increment in supercolony size and extreme unicolonial behaviour of Argentine ant introduced populations decreases intraspecific competition and enhance interspecific competitive ability (Holway 1999, Holway and Suarez 2004, Walters and Mackay 2005), which severely decreases the abundance and diversity of native ant fauna and contributes to its success as an invader (Passera 1994, Heller 2004).

The widespread success of the Argentine ant causes enormous ecological and economic impacts in its introduced ranges. As already pointed out, one of the most notable effects of the invasion is the displacement of nearly all native ant fauna (Way et al. 1997, Kennedy 1998, Carpintero et al. 2005), which plays a major role in several ecological processes (Gómez et al. 2003, Oliveras et al. 2005). Changes in the original ant composition have disrupted ant-plant mutualisms (Bond and Slingsby 1984, Gómez and Oliveras 2003), altered arthropod communities (Cole et al. 1992, Bolger et al. 2000), and disturbed populations of some vertebrate species (Suarez et al. 2000, Gómez and Espadaler 2004, Roca 2004). From an economic perspective, Argentine ants may be a major pest around human residences, especially during cold winters or extreme hot summers (Gordon et al. 2001). Agricultural activities can be considerably affected by the Argentine ant, directly by damaging infrastructures (such as making holes in plastic drip tubes) or indirectly disrupting insects' ecological function (such as tending honeydew-producing insects against predators) (Haney et al. 1987, Vega and Rust 2001).

Due to the ant's widespread distribution and the difficulties in eradicating introduced populations once established, the adoption of preventive measures appears to be the best and most logical strategy to control Argentine ant invasion (Holway et al. 2002a). However, since preventing the accidental transport of the species is almost impossible, determining those geographic areas most susceptible to invasion will help detect them in novel areas where effective isolated measures can be adopted at a minimal cost for the ecosystem (McGlynn 1999). A better knowledge of the abiotic and biotic factors governing the environmental range and determining the geographic variation of the Argentine ant would enormously contribute to establishing integrated management policies, which would consequently reduce the negative ecological effects of the invasion.

Until now, several studies have assessed the influence of abiotic factors on the Argentine ant invasion in most Mediterranean areas around the world. In its native range, the Argentine ant is commonly found along the major rivers in the subtropical Paraná River drainage basin, both in natural habitats and urban settlements along major rivers (Tsutsui et al. 2001, Wild 2004). Since invaders tend to occupy areas matching similar abiotic environmental conditions to the original range (Simberloff 1989), the Argentine ant appears to be more successful in subtropical and Mediterranean climates than in extreme cold, arid and tropical climates (Hölldobler and Wilson 1990, Passera 1994). However, under extreme adverse conditions it may also persist near human habitations (Suarez et al. 2001). Throughout its introduced range the Argentine ant is mainly found near anthropogenic disturbed areas, though it also occupies a wide variety of natural habitats around the world (Holway 1995, Suarez et al. 2001, Vega and Rust 2001).

Although these requirements tend to vary across spatial and temporal scales (Wiens 1989, Holway et al. 2002a), studies at local scales associate Argentine ants to cool and moist habitats along the coast and inland mesic areas (Holway 1998). Soil moisture and water presence seem to be determinant for its establishment and further spread into novel areas, especially in drier and hotter environmental conditions where the invasion expands through riparian corridors (Holway 1995, Human et al. 1998, Menke and Holway 2006). Moreover, since *L. humile* appears active in a wider range of seasonal and thermal conditions than native ant species (Human et al. 1998, Abril 2005), the high exploitation competition of Argentine ant may reduce the foraging success of native colonies and facilitate its expansion (Sanders et al. 2001). Other factors such as vegetation type, soil characteristics, altitude and degree of disturbance have also been indicated as influencing the invasion process (Way et al. 1997, Paiva et al. 1998). Simberloff (1989) and Holway (1998), however, suggested that the association of some abiotic factors with the presence of the Argentine ant could be due to correlational rather than causal relationships. In this sense, besides the widespread thought that Argentine ants prefer low-altitudinal areas and human-disturbed habitats near the coast, their actual geographic distribution could be mostly explained by their jump dispersion associated to humans and by the earliest stage of the invasion in some areas (Holway 1995, Suarez et al. 2001, Carpintero et al. 2005, Krushelnycky et al. 2005).

Despite the previous studies determining the role of abiotic environmental conditions on the Argentine ant spread, few of these have assessed the biogeographic dimensions of the invasion. Suarez et al. (2001) were the first to successfully estimate the occurrence of the species at global scales, summarizing and/or complementing the available data from its native range (Tsutsui et al. 2001, Wild 2004) and other invaded areas worldwide (Giraud et al. 2002, Holway et al. 2002b, Espadaler and Gómez 2003, Ward et al. 2005). With the increase in occurrence data available on geographic distribution and rates of spread, some authors have estimated the Argentine ant potential ranges using predictive models at local scales (Hartley and Lester 2003, Krushelnycky et al. 2005) and at global scales (Hartley et al. 2003, Hartley et al. 2006). However, since none of them performed a sound analysis of its potential worldwide distribution and studies at large spatial scales are crucial to determine the geographic extent of the invasion (Holway et al. 2002a), the present PhD thesis attempts to address this lack of knowledge through modeling the ecological niche of the Argentine ant.

Ecological niche models

Ecological niche models (also referred to as climate-matching envelope, species distribution models, or other related names (Pearson and Dawson 2003, Guisan and Thuiller 2005, Soberón and Peterson 2005)) represent only one step in understanding the complex phenomenon of invasions (cf. pages 15-16), but it provides an excellent assessment of the potential geographic dimensions of the phenomenon (Peterson 2003).

The concept of *ecological niche* was first used by Grinnell (1917) to designate the ultimate distributional unit of a species, conceived as the geographic area within which an organism can survive in the absence of other organisms. Simultaneously, other researchers (Elton 1927, Gause 1934) conceived the ecological niche as the role of a species in an ecological community. Both conceptions were integrated by Hutchinson (1957), who redefined the niche as an n-dimensional space or hypervolume delimiting the total environmental range within which a species is able to survive and reproduce indefinitely. Each dimension of this hypervolume corresponds to an environmental gradient along which an organism presents different tolerance ranges. Hutchinson also differentiated between fundamental and realized ecological niches: the *fundamental niche* is the entire set of abiotic conditions that a species could occupy in the absence of biotic influences, while the *realized niche* is the real set of conditions in which the species actually exists given the presence of other species. Since competition and interactions prevent species from occupying the whole fundamental niche, the realized niche usually represents a smaller set of this overall potential hypervolume (Giller 1984).

Differentiating between fundamental and realized niches is particularly important in the context of ecological niche modeling practices (Pulliam 2000). Some niche models correlate environmental abiotic variables influencing species' ecology with present-day observed distribution to identify areas suitable for the species (*correlative approach*). Since current species distribution is not only constrained by abiotic factors but also by biotic interactions, correlative niche-models are thus likely to predict the realized ecological niche. Other niche models use direct measures of individuals' physiological response to environmental conditions (*mechanistic approach*), in some way estimating the fundamental niche of the species. Strict mechanistic approaches can additionally incorporate biotic interactions to finally predict the realized niche of the species (Guisan and Zimmermann 2000, Pearson and Dawson 2003, Soberón and Peterson 2005). A detailed discussion on the main limitations affecting ecological niche models, and also on the advantages and disadvantages of both correlative/mechanistic approaches, is extensively summarized in Pearson and Dawson (2003). However, I will briefly present the most relevant ideas in the next paragraphs.

Regardless of the modeling approach, ecological niche models present a series of inherent limitations to correctly predict the distribution of a species (Guisan and Zimmermann 2000, Pearson and Dawson 2003, Guisan and Thuiller 2005). The geographic range of a species is the result of the complex relationship between its ecology and evolutionary history (Pulliam 2000, Wiens and Graham 2005), determined by different factors and processes acting at different scales (Wiens 1989). So, in relation to these factors (following Soberón and Peterson (2005)), the main limitations of niche models are:

(i) abiotic conditions (which reflect the physiological tolerance of the species in the area) considered in niche models may not necessarily be the most relevant in determining species presence, as those having the greatest influence are not available.
(ii) biotic interactions (through competition, predation, mutualisms, parasitism, etc.) alter species distribution by restricting or enhancing certain processes, so that models developed on abiotic factors alone may produce incorrect predictions.
(iii) restrictions to species dispersal (not only due to species' characteristics, but also to landscape configuration) also suppose an important limitation, since actual distributions cannot reflect the overall *potential distribution* range of species. This limitation is extremely evident with biological invasions, because present-day distributions of most invasive species are at an early stage of the invasion process.
(iv) niche models assume that changes in the species' capability of adapting to new environments occur at long-term temporal scales, thus conserving the same fundamental niche in different geographic areas and under future climate changes (Peterson et al. 1999). However, rapid evolutionary changes can certainly occur and thus reduce the predictive capacity of niche models.

Besides these common reservations, there are some extra limitations depending on the approach adopted to model ecological niches (Guisan and Zimmermann 2000, Pearson and Dawson 2003). The major criticism of the correlative approach is that species distribution may not be in equilibrium with its environment (as happens with most invasive species) due to biotic interactions, dispersal characteristics, and human management of the landscape, and thus correlative niche models may not predict the full range of the species' realized niche. Contrarily, since mechanistic models do not assume equilibrium or a relationship between species occurrence and environmental data, models based on physiological restrictions to species ranges are expected to identify the absolute environmental limits more precisely. However, mechanistic models have other limitations (such as the fundamental niche often does not provide information on the current distribution of a species, individuals of a species may show different tolerance ranges, and rapid evolutionary changes may modify the fundamental niche) that restrict its predictive capacity to estimate the species' fundamental niche (Guisan and Zimmermann 2000, Pearson and Dawson 2003, Soberón and Peterson 2005).

Despite the limitations of correlative and mechanistic niche models have when dealing with the enormous complexity of ecological systems, the importance of niche modeling practices must not be underestimated. When applied at an appropriate scale and correctly interpreted taking into account their inherent constraints, niche models provide a valuable assessment of the geographic dimensions of species distribution. Moreover, they allow us to describe changes in species' distributions under future scenarios of climate or land-use change and anticipate the establishment of invasive species in new geographic areas. Bearing in mind the assumptions and limitations presented above, and that correlative models are more appropriate at global and regional scales than mechanistic models (which seem to be more accurate at finer spatial scales) (Richardson et al. (2004) in Beever et al. (2006)) (Guisan and Zimmermann 2000), the approach finally adopted in this PhD thesis for estimating the Argentine ant distribution has been the correlative approach, hereafter called niche-modeling approach to simplify reading the manuscript.

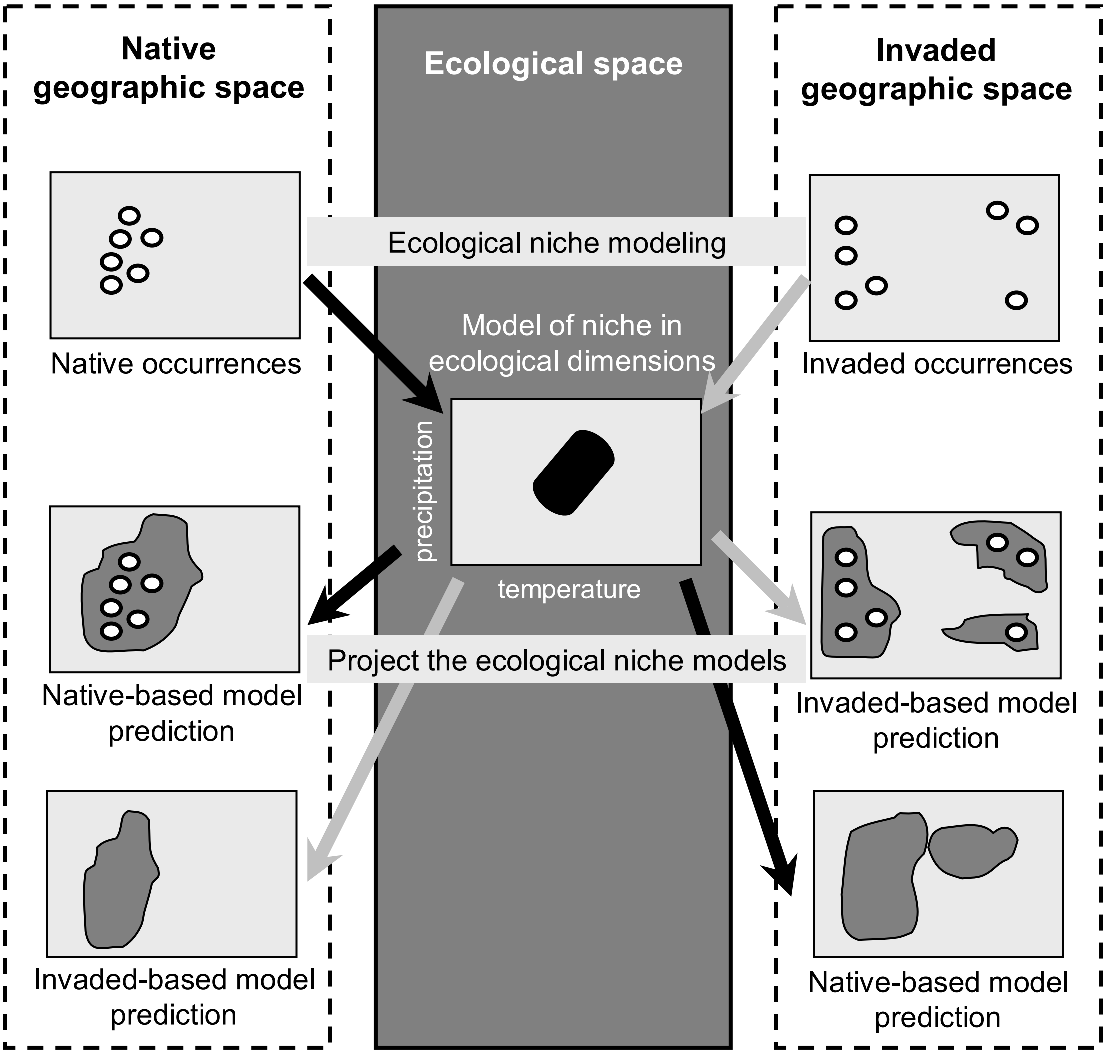

Figure 4 Diagram of an ecological niche modeling practice for an invasive species between native and invaded geographical areas (modified from Peterson (2003)). First, ecological niche requirements are modeled in ecological space based on native occurrence data, and then projected back onto the native geographic area and onto the invaded range to identify areas susceptible to invasion. Finally, the same process is also repeated using occurrence data from the invaded area.

Many niche-modeling approaches have been used to predict the geographic distribution of invasive and non invasive species, including multiple regression analysis, neural networks, genetic algorithms, and several others (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith et al. 2006). As already mentioned, all these approaches are based on correlations between occurrence data and environmental characteristics influencing species presence. Once developed, niche models are then projected back onto the landscape to identify areas presenting similar ecological conditions, and thus estimate the geographic dimensions of the invasion (for more details on the steps of model building see Guisan and Zimmermann (2000) and Guisan and Thuiller (2005)). Niche models for invasive species can be developed within the species' native range and then projected to other nonnative regions (Peterson 2003, Thuiller et al. 2005), or, on the contrary, built up on occurrence and environmental correlations within the non-native ranges (Drake and Lodge 2006) (Figure 4). Both approaches have their advantages and drawbacks: while native-based models rely on the fact that the species is in equilibrium with its environment and thus consider the overall realized niche of the species, invaded-based models take into account possible rapid evolutionary changes occurred after introduction (Peterson 2003).

A hierarchical niche modeling framework

Coincident with the growth of research and management strategies focused on biological diversity and more specifically on biotic invasions, there has been an increasing awareness regarding the need to explicitly incorporate scale into ecological studies (Beever et al. 2006). Distributional patterns in ecology are eminently scale-dependent, since their underlying process and mechanisms differ considerably across scales (Wiens 1989, Levin 1992, Mackey and Lindenmayer 2001, Farina et al. 2005). The concept of scale generally refers to the spatial or temporal dimension of an organism or process, characterized by both grain and extent (Farina 1998). The present study considers scale as the spatial dimension, where grain refers to the lowest limit of spatial resolution (pixel size for raster data) of a given data set, and extent the size of the study area. According to these two components, ecological studies also categorize the concept of scale as fine scale (referring to small resolution and reduced study areas) or broad scale (referring to coarse resolutions and large study areas) (Turner et al. 1989).

Predicting a species' potential distribution via ecological niches necessarily presupposes reducing the multi-dimensional natural environment into a few scales due to our limited perceptual capabilities and technical constraints (Levin 1992). To select the most appropriate scale and factors for modeling the phenomenon of study, Pearson and Dawson (2003) proposed a modeling framework where factors determining species' distribution operates in a hierarchic manner from global to local scales (Figure 5): at global scales climate appears to be the dominant factor determining species distribution, while at regional to local scales topography and land-use become more important; however, biotic interactions and microclimate factors finally shape species distribution at the finest scales (Willis and Whittaker 2002, Pearson and Dawson 2003). This hierarchical framework relies on the interconnection between the different levels of a system, in which the higher levels constrain the lower levels and vice versa (Pearson and Dawson 2003). Ecological systems are good examples of hierarchical structures where different levels operate across spatial and temporal scales, and the importance of ecological processes varies according to the scale (O'Neill et al. 1989, Turner et al. 1989). Thus, in the context of niche models, abiotic factors (such as climate and topography mainly) seem to be more influential at global and regional scales than biotic factors, which occupy lower levels in the hierarchy and therefore become more limiting when higher level conditions are satisfied (Willis and Whittaker 2002).

From this point of view, the selection of the appropriate spatial scale and environmental factors for predicting species distribution is of extreme importance in order to obtain accurate results. As such, a better understanding of the complex interactions between species distribution and those influencing factors across spatial scales is thus required to produce reliable and accurate estimations of the geographic dimensions of the species' ranges (Levin 1992).

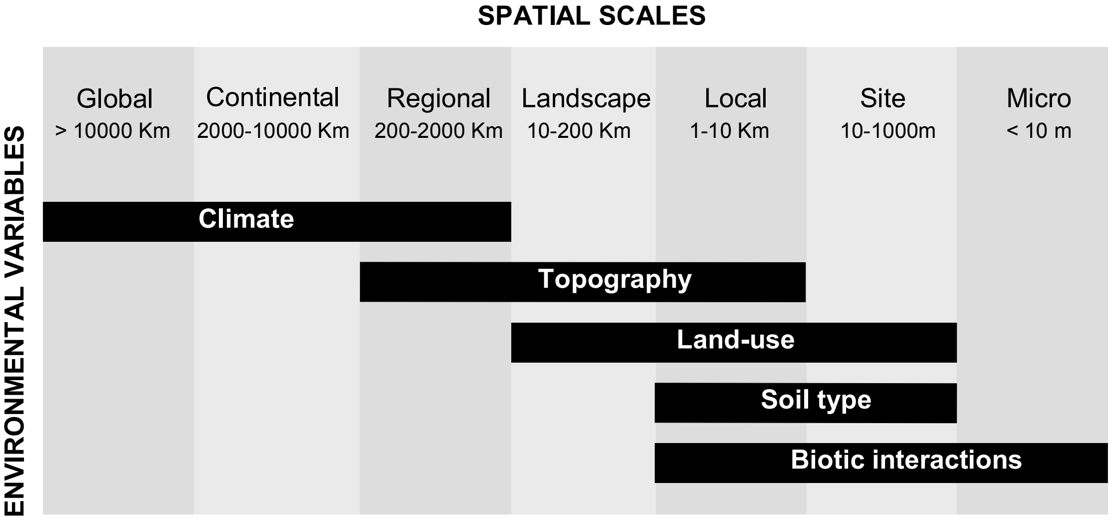

Figure 5 Diagram of the hierarchical modeling framework proposed by Pearson and Dawson (2003), which shows the influence of different environmental factors on species distribution across several spatial scales. Large spatial extents are associated with coarse data resolution, and small extents with fine data resolution (modified from Pearson and Dawson (2003))

Objectives

The major aim of this study is to assess the geographic dimensions of Argentine ant invasion using different methodologies of correlative niche modeling approaches, but also to explore key characteristics of complex species-environmental relationships influencing species distribution across several scales and under different temporal and geographic scenarios. The adoption of such a multi-scalar approach for modeling the invasion process is crucial for elucidating the invasiveness and to establish efficient management strategies for Argentine ant prevention and control (Pauchard and Shea 2006).

Chapter 2 aims to determine the potential geographic distribution of the Argentine ant at broad spatial scales in the present and also in the future, to consider the effects of climate change on the invasion process. Ecological niche models will be developed using the Genetic Algorithm for Rule-set Production (GARP), and a series of occurrence and environmental data determining species distribution. Future changes in the geography of the species will be assessed using different general circulation models scenarios of future climates.

Once the worldwide distribution of the species at global scales will be established, the goal of **Chapter 3** is to assess changes in the species ecological niche after introduction as a further factor explaining the highly invasive potential of the Argentine ant in new invaded areas. With this aim in mind, a cross-prediction analysis will be performed at regional scales using GARP between native range, the United

States of America, Japan and the Iberian Peninsula, searching for possible dissimilarities in the species ecological niche niche. In relation to the topic of this chapter, Holway et al. (2002a) highlighted the relevance of comparisons between native and introduced populations of invasive ant species to clarify some unresolved questions on the ecology and geographic origins of the invasion.

At regional scales, in **Chapter 4**, we will also perform a cross-prediction analysis within the Iberian Peninsula to elucidate possible ecological and/or geographical differences between the invasive patterns of the Argentine ant on eastern and western sides (related to Mediterranean and Atlantic influences, respectively). The comparison was made using three different modeling techniques: the Genetic Algorithm for Rule-set Production (GARP), Maximum Entropy Model (Maxent), and Generalized Linear Models (GLM), to increase the agreement between predictions and reality by selecting consensual trends of species distributional patterns among modeling approaches, and also for the methodological interest itself.

Fnally, **Chapter 5** aims to model Argentine ant distribution at regional (Catalonia) and local scales (Costa Brava) using Generalized Additive Models (GAM). At this stage three main hypotheses will be tested: (i) the role of ecological characteristics is not symmetrical at regional and local scales, (ii) latitudinal differences do exist along the Costa Brava, and finally (iii) invasive patterns are specific in the coastal versus the inland areas.

Each chapter of the dissertation is conceived as an independent study, although together they constitute the multi-scalar analysis of the Argentine ant's geographic distribution. Each chapter presents the standard structure of a journal article, since the final aim is scientific publication. Indeed, the second chapter has already been published, the third is now in press, and the fourth has recently been submitted to a peer-review journal. As a result of this structure, parts of the introduction and methods sections may present some similarities across several chapters, but I preferred to keep the full text in order to contextualize each study. At the end, however, the reader can find a General discussion (**Chapter 6**) on the overall results, and the main conclusions of the study on Argentine ant geographic distribution across several spatial scales.

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Chapter 2

Geographic potential of Argentine ants (*Linepithema humile* Mayr) in the face of global climate change

Roura-Pascual, N., A.V. Suarez, C. Gómez, P. Pons, Y. Touyama, A. L. Wild, and A.T. Peterson. Proc. R. Soc. Lond. B. (2004) 271:2527-2535

CHAPTER 2

Geographic potential of Argentine ants (*Linepithema humile* Mayr) in the face of Global climate change

Abstract

Determining the spread and potential geographic distribution of invasive species is integral to making invasion biology a predictive science. We assembled a dataset of over 1000 occurrences of the Argentine ant (*Linepithema humile*), one of the world's worst invasive alien species. Native to central South America, Argentine ants are now found in many Mediterranean and subtropical climates around the world. We used this dataset to assess the species' potential geographic and ecological distribution, and to examine changes in its distributional potential associated with global climate change, using techniques for ecological niche modeling. Models developed were highly predictive of the species' overall range, including both the native distributional area and invaded areas worldwide. Despite its already widespread occurrence, *L. humile* has potential for further spread, with tropical coastal Africa and Southeast Asia apparently vulnerable to invasion. Projecting ecological niche models onto 4 general circulation model (GCM) scenarios of future (2050s) climates provided scenarios of the species' potential for distributional expansion with warming climates: generally, the species was predicted to retract its range in tropical regions, but to expand at higher latitude areas.

Introduction

Global environmental change alters the spatial distribution of physical conditions, habitats, and species on Earth (Chapin et al. 2000). With widespread ecological impacts, biological invasions are a significant component of human-caused global environmental change (Vitousek et al. 1996). Understanding the biology of invasive species and their potential geographic distributions is essential to anticipating their large-scale and long-term effects (Tsutsui et al. 2001). Despite the widely acknowledged need for making invasion biology a more predictive science (Perrins et al. 1992, Carlton 1996, Kareiva 1996, Williamson 1996, NAS 2002), relatively few studies have modeled the potential ecological distribution of invasive species (Mack et al. 2000, Hulme 2003, Peterson 2003).

Invasive ants have many negative impacts on ecological communities in their introduced ranges (Holway et al. 2002a), making them key in conservation efforts (McGlynn 1999, Holway et al. 2002a). The Argentine ant (*Linepithema humile*) is a widespread invader (http://www.issg.org/database); native to South America, it is now established in at least 15 countries on six continents and many oceanic islands (Suarez et al. 2001). Although associated with human-modified habitats throughout its nonnative range, Argentine ants can also colonize natural areas with low anthropogenic disturbance (De Kock and Giliomee 1989, Holway 1998, Suarez et al. 2001, Gómez and Oliveras 2003). Worldwide, *L. humile* has impacted native ant faunas, leading to changes in arthropod communities, ant-vertebrate interactions, and ant-plant relationships, as well as economic effects, such as food contamination and damage to infrastructure (Bond and Slingsby 1984, Cole et al. 1992, Human and Gordon 1996, Suarez et al. 1998, Suarez et al. 2000, Vega and Rust 2001, Holway et al. 2002a, Gómez and Oliveras 2003, Touyama et al. 2003). In spite of the numerous studies of *Linepithema humile*, little research has focused on its ecological and geographic distribution at broad spatial scales (Tsutsui et al. 2000, Suarez et al. 2001, Tsutsui et al. 2001, Hartley et al. 2003, Wild 2004), and no study has yet assessed likely changes in its global distributional potential associated with global climate change[3].

Here, we use the Argentine ant as a model system to develop predictive models of an invader's potential global range. We compiled a data set of 1000+ known occurrences to examine the Argentine ant's potential geographic distribution, and explore the consequences of global climate change on its distribution under various scenarios of climate change for the next 50 years.

Methods

Ecological niche models are based on non-random correlations between known occurrences of species and environmental data sets that describe parameters ostensibly related to the dimensions of the ecological niche of the species. We developed ecological niche models for Argentine ant potential distributions based on two independent environmental data sets; differences in their origin and resolution make combination difficult, but similarities in results based on such distinct data sets provide an excellent indication of robustness of results. Occurrence data were used to determine that the species' native distribution was centered along major river systems in northeastern Argentina and southern Paraguay (Tsutsui et al. 2001, Wild 2004). This area was carefully delineated to avoid accidental inclusion of related species of *Linepithema* (Wild 2004).

Data sets.-- Overall, we used 1007 occurrence points drawn from data associated with specimens in natural history museums and personal collections; scientific literature; and onsite field surveys (see Annexes 1 and 2). Models were based on 67 occurrence points that are putatively from the species' native range; because of the potential for misindentifications even in the native range, we used only those localities visited personally by the authors and/or verified in ongoing taxonomic research by one of the authors (Wild 2004). A set of 940 occurrence points from other areas (i.e., invaded areas) was withheld from model-building, and used only for an extrinsic evaluation of final predicted potential invasive distributions (as not all of these localities have been reviewed personally by the authors, some misidentifications may exist). Likewise, 31 sites that represent putative absences within or close to the native range established in onsite visits by the authors or in detailed faunal studies were used in tests of model accuracy. All occurrence data are provided in Annexe 1.

The two environmental data sets (in the form of digital maps, or 'coverages') differed in the variables summarized, spatial resolution, and interpretability. The first, with relatively coarse spatial resolution, included 15 coverages summarizing aspects of topography (elevation, topographic index, slope, aspect, flow direction and flow accumulation, from the US Geological Survey's Hydro-1K data set[4]; native resolution 1 x 1 km) and climate (annual means of diurnal temperature range; frost days; precipitation; maximum, minimum and mean temperatures; solar radiation; wet days; and vapor pressure; for 1960-1990 from the Intergovernmental Panel on Climate Change[5]; native resolution 50 x 50 km). To minimize conflicts in scale between

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[3] Posterior to the publication of this chapter, a new study analyzing the worldwide potential distribution of the Argentine ant has appeared: "Hartley, S., Harris, R., & Lester, P.J. (2006) Quantifying uncertainty in the potential distribution of an invasive species: climate and the Argentine ant. Ecology Letters, 9, 1068-1079."

[4] http://edcdaac.udgs.gov/gtopo30/hydro/

[5] http://www.ipcc.ch/

topographic and climatic data, we conducted analyses at an intermediate resolution (10 x 10 km). As several of the coverages derived from the topographic data (e.g., topographic index, flow direction, and flow accumulation) were not available for Australia, we developed separate (but parallel) models for that continent simply omitting the coverages that were lacking.

The second data set, with a somewhat finer overall native resolution, included 18 coverages: the same topographic variables listed above, plus monthly remotely-sensed data layers summarizing the Normalized Difference Vegetation Index (NDVI) as measured by the Advanced Very High Resolution Radiometer (AVHRR) satellite[6] (native resolution 8 x 8 km) for 1999, matching the modal date of the occurrence data used. Such composites of AVHRR imagery and topographic data have been shown to be effective data inputs for fine-scale predictions of species' distributions (Egbert et al. 2002, Peterson et al. 2004). Because AVHRR data were unavailable at high latitudes, we eliminated such (>60°) areas from consideration. To account for differences in summer-winter timing between Northern and Southern hemispheres, and given the monthly nature of the AVHRR data, we shifted Southern Hemisphere monthly data by 6 months, thereby aligning northern and austral summers and winters appropriately.

All of the manipulations described below except climate-change projections, which were possible only for climate-based analyses, were repeated for both environmental data sets. Throughout, we refer to the two data sets as "climate" data and "NDVI" data, respectively. Models were developed across central-eastern South America, and projected worldwide to explore geographic implications.

Niche modeling.-- Our approach is based on modeling species' ecological niches (Peterson et al. 2002b, Stockwell and Peterson 2002, Peterson et al. 2003), which have been shown to constitute long-term stable constraint on species' potential geographic distributions (Peterson et al. 1999, Peterson et al. 2001, Martínez-Meyer 2002, Peterson et al. 2003). Ecological niches are herein defined as the set of conditions under which a species is able to maintain populations without immigration (Grinnell 1917, 1924). Several avenues of research have demonstrated widespread evolutionary conservatism in niche characteristics (Peterson et al. 1999, Martínez-Meyer 2002), allowing accurate predictions of invasive species' potential distributions (Peterson 2003). Ecological niche characteristics represent but one factor in the complex phenomenon of invasions, which includes (1) dispersal and colonization of new areas, (2) establishment of non-native populations, (3) the ecological appropriateness of new areas (i.e., does the area fit the species' niche requirements?), and (4) population expansion and spread across these areas; therefore, while ecological niche modeling cannot explain the entire invasion process, it does provide an excellent assessment of the potential geographic dimensions of the phenomenon (Peterson 2003).

Our approach consisted of five steps. (1) Model the ecological niche requirements of the species based on known occurrences on the native distribution area of the species. (2) Test the accuracy of the native-range predictions. (3) Project the niche model onto other regions to identify areas susceptible to invasion. (4) Test to validate predictions in other regions. (5) Project niche models onto scenarios of future climate change to predict potential distributional shifts (Peterson et al. 2001, Peterson et al. 2002a, Peterson and Shaw 2003).

The software tool used for niche modeling was the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell and Peters 1999). GARP uses a genetic algorithm to search for non-random associations between environmental variables and known occurrences, as contrasted with the environmental characteristics of the overall study area. Occurrence points (as longitude-latitude coordinates) are mapped onto a spatial grid, and combined with environmental variables (in the form of digital maps, or

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[6] http://glcf.umiacs.umd.edu/data/landcover/

'coverages') in an evolutionary computing environment to develop a model of the species' ecological niche. The resulting model is then used to classify the entire study area to identify areas modeled as suitable. Although these environmental variables cannot represent all possible ecological-niche dimensions, they likely represent or are correlated with many influential ones in delineating the species' potential distribution. Previous tests of GARP have shown successful predictions of distributional phenomena for numerous taxa and regions (Peterson 2001, Peterson et al. 2002a, Peterson and Kluza 2003).

Available occurrence points (67, in the present case) are resampled with replacement to create a population of 1250 presence points; an equivalent number of points is resampled from the population of grid squares ('pixels') from which the species has not been recorded. These 2500 points are divided equally into training (for creating models) and testing (for evaluating model quality) data sets (Anderson et al. 2003). Resampling occurrence points reduces effects of sampling biases, such as omission, spatial bias, or imbalances in available occurrence data (Stockwell and Peters 1999).

Models are composed of a set of conditional rules developed through an iterative process of rule selection, evaluation, testing, and incorporation or rejection. First, a method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic rules, etc), and applied to the training data set. Then, a rule is developed by a number of means mimicking DNA evolution: point mutations, deletions, crossing over, etc., to maximize predictive accuracy. Rule accuracy is evaluated via the testing data, as a significance parameter based on the percentage of points correctly predicted as present or absent by the rule. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the final rule-set. The algorithm runs either 1000 iterations or until addition of new rules has no effect on predictive accuracy. The final rule-set, or ecological niche model, is then projected onto a digital map to identify a potential geographic distribution (Stockwell and Peters 1999).

Spatial predictions of presence and absence can hold two types of error: omission (areas of known presence predicted absent) and commission (areas of known absence predicted present) (Fielding and Bell 1997). To achieve highest predictive accuracy and simultaneously achieve a most general result (i.e., able to be extrapolated to other conditions and regions), prior to modeling, we reduced each environmental dataset to just those coverages contributing positively to model quality using a jackknife procedure (Peterson and Cohoon 1999). We systematically omitted 1-3 coverages at a time, and calculated Pearson product-moment correlations between inclusion-exclusion of a particular coverage and omission error in each resulting model (Peterson and Cohoon 1999, Peterson et al. 2003). Coverages presenting a positive correlation on the order of $r > 0.08$ were removed from further analysis, and modeling thus focused on those data coverages that contribute positively to models' having low omission rates.

Because GARP does not produce unique solutions, we followed recently published best practices approaches to identifying an optimal subset of resulting replicate models (Anderson et al. 2003). For each analysis, we developed 1000 replicate models; of these models, we retained the 200 models with lowest omission error. Finally, we retained the 100 models with moderate commission error (i.e., we discarded the 100 models with area predicted present showing greatest deviations from the overall median area predicted present across all models). This 'best subset' of models was summed to produce final predictions of potential distributions.

To validate our model predictions, we compared their ability to predict independent sets of test points with that expected under random models by two methods. In the native distributional area in which data on both presences and absences were available, we used the more robust kappa approach (Congalton and

Green 1999, Jenness and Wynne 2005). We had 31 absence points and 75 presence points, including the 67 native range points plus 8 presences from closeby areas that apparently represent introductions. We calculated the KHAT statistic using a custom ArcView 3.x extension (Jenness and Wynne 2005). Because test results depend critically on how occurrence points are divided into training and testing data sets (Fielding and Bell 1997), we used a checkerboard approach that presents a maximum challenge to the model—prediction into areas from which no occurrence information was available (Peterson and Shaw 2003). Native distribution localities were classified into two categories depending on their location on a 2° x 2° checkerboard grid. Ecological niche models based on localities in one category were used to predict the distribution of the other occurrence category and vice versa.

We then projected these validated native-range ecological niche models onto landscapes worldwide to evaluate the species' invasive potential. On invaded distributional areas, given that absence data were not available, models were validated via chi-square tests (Peterson et al. 2003, Peterson and Shaw 2003) that incorporate dimensions of correct prediction of both presences (based on independent test data) and absences (based on expected frequencies) (Stockwell and Peters 1999, Anderson et al. 2003). Here, random expectations were calculated as the product of the proportional area predicted present and the number of test presence points. Observed frequencies of correct and incorrect predictions of presence were then compared using a χ^2 test (1 df). Given that sampling of invaded distributions was highly biased towards certain regions (western Europe, North America), in addition to worldwide tests, we carried out more conservative chi-square tests specifically in those densely-sampled regions, buffering known occurrences by 500 km to determine areas for tests.

Finally, we developed ecological niche models for extrapolation to future climates to predict the species' potential future distribution. Because fewer environmental dimensions are available for changed-climate scenarios, these models were of necessity based on a somewhat reduced set of climate coverages (precipitation, and minimum, mean and maximum temperature) plus topography. Once again, to reduce dimensionality of analyses, we performed a jackknife manipulation. Ecological niche models developed were projected onto future climate data sets (2050s) (Peterson et al. 2001) derived from two general circulation models: CGCM2 developed at the Canadian Center for Climate Modelling and Analysis, and HadCM3 at the Hadley Center for Climate Prediction and Research. Two emissions scenarios (A2 and B2) were used: B2 scenarios (CGCM2B2 and HadCM3B2) assume 0.5%/year CO_2 increase and incorporate sulphate aerosol forcing, making them relatively conservative, whereas A2 scenarios (CGCM2A2 and HadCM3A2) assume a 1%/year CO_2 increase and do not take into account effects of sulfate aerosols, and are thus more severe.

Results

Native distribution

Native-distribution occurrence points were distributed principally in northern Argentina and southern Paraguay along major river systems (Río Paraná, Río Paraguay, and Río Uruguay). The jackknife manipulation for the climate data lead us to exclude 7 coverages, leaving minimum and mean annual temperatures, precipitation, diurnal temperature range, wet days, flow accumulation, and flow direction for modeling (none with inclusion strongly positively associated with increased omission error). Best-subsets models developed based on these data sets predicted fairly continuous Argentine ant distribution from eastern Bolivia to Uruguay, through northeastern Argentina, Paraguay, and southern Brazil (Figure 1).

For the NDVI data set, the jackknife manipulation identified the following coverages for further analysis: elevation, topographic index, and NDVI coverages for January, March, April, July, August, and October (none with inclusion strongly positively associated with omission error). Best-subsets NDVI-based models predicted smaller native-range areas (7-9% smaller areas depending on cut-off used for presence) than the climate-based models.

Both models predicted well the species' distribution in unsampled regions based on the two reciprocal checkerboard tests. Test sample sizes available were 44 and 23 for the two reciprocal tests. Overall accuracy measures for the two climatic models were 84-87%, and KHAT values were 0.68-0.74; for NDVI models, accuracies were 87-89%, and KHAT values 0.71-0.75. Because KHAT ranges from -1 to +1, these results suggest excellent agreement between model predictions and actual distributional patterns. Comparisons of kappa statistics and associated variances between the two environmental data sets indicated that they were not significantly different ($P > 0.3$). As such, these two environmental data sets can be considered complementary, producing approximately equal classifications.

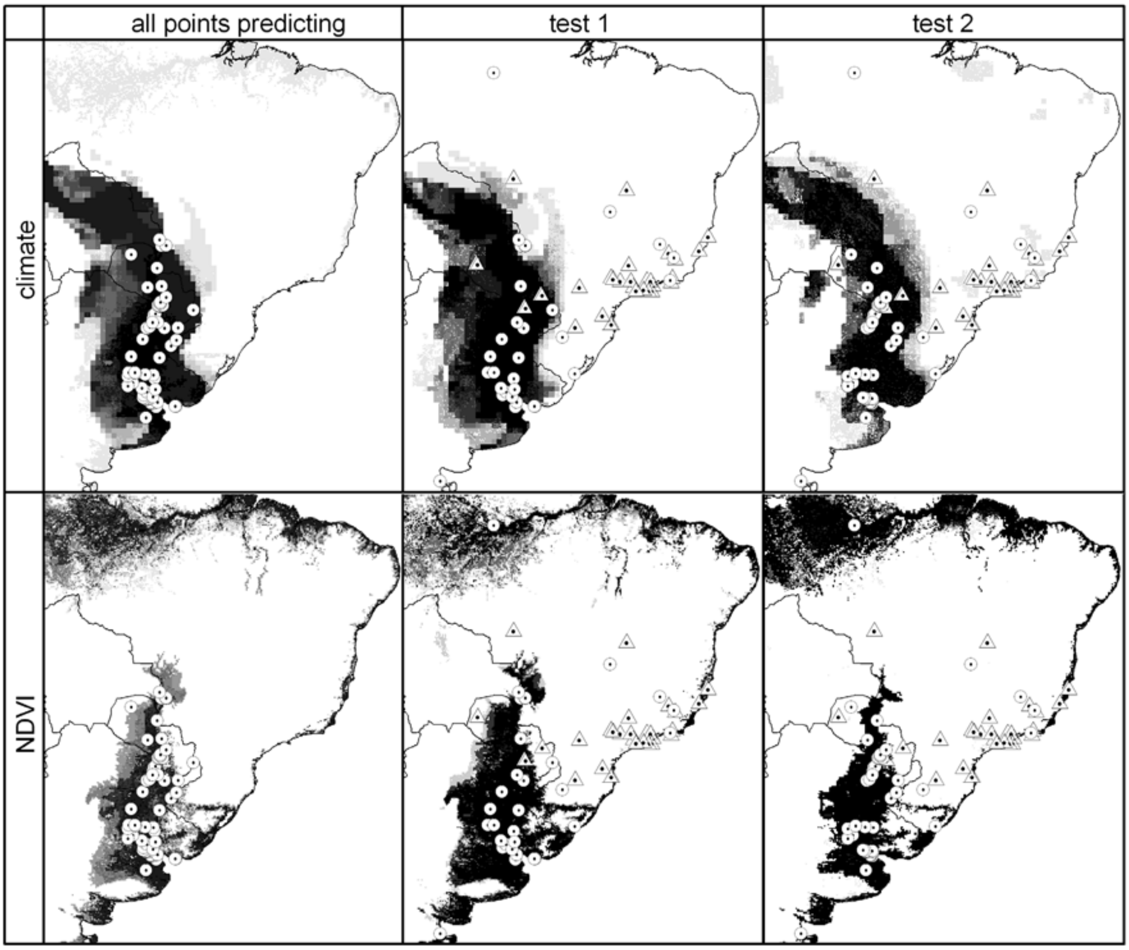

Figure 1 Illustration of tests used to assess model predictivity for two environmental data sets (climate and NDVI). Occurrence data for the Argentine ant in the native range were divided into two categories depending on their position in relation to a grid of 2º x 2º. Independent occurrence data are overlaid in each prediction, presences in dots and absences in triangles. The first column presents predictions based on all native occurrence data combined, and second and third columns present predictions based on the two reciprocal spatial subdivisions of the available native occurrence data, with appropriate test data set overlaid. Darker shading indicates greater model agreement in predicting potential Argentine ant presence.

Invaded distribution

Given that ecological niche models based on both environmental data sets yielded highly accurate predictions of the native distribution, we projected them worldwide. For climate-based models, areas outside the native distribution with the most suitable conditions were the west coast and southeast of the United States, Mediterranean coast, central and southern Africa, western Madagascar, parts of central Asia (e.g., Kazakhstan), western India, a band from northeastern India to Thailand, northeastern China, Korea, southern Japan, coastal Australia, and New Zealand (Figure 2a). NDVI-based models predicted similar patterns of potential distribution, although generally in more restricted areas. Climate-based models predicted areas of potential distribution in the central United States, northern Bolivia, and central Africa, at difference with NDVI-based models, whereas NDVI-based models predicted areas at northern latitudes, along the Amazon River, and in central Australia at difference with the climate-based models (Figure 2b). Coincident areas in predictions of both climatic and NDVI models are shown in Figure 2c.

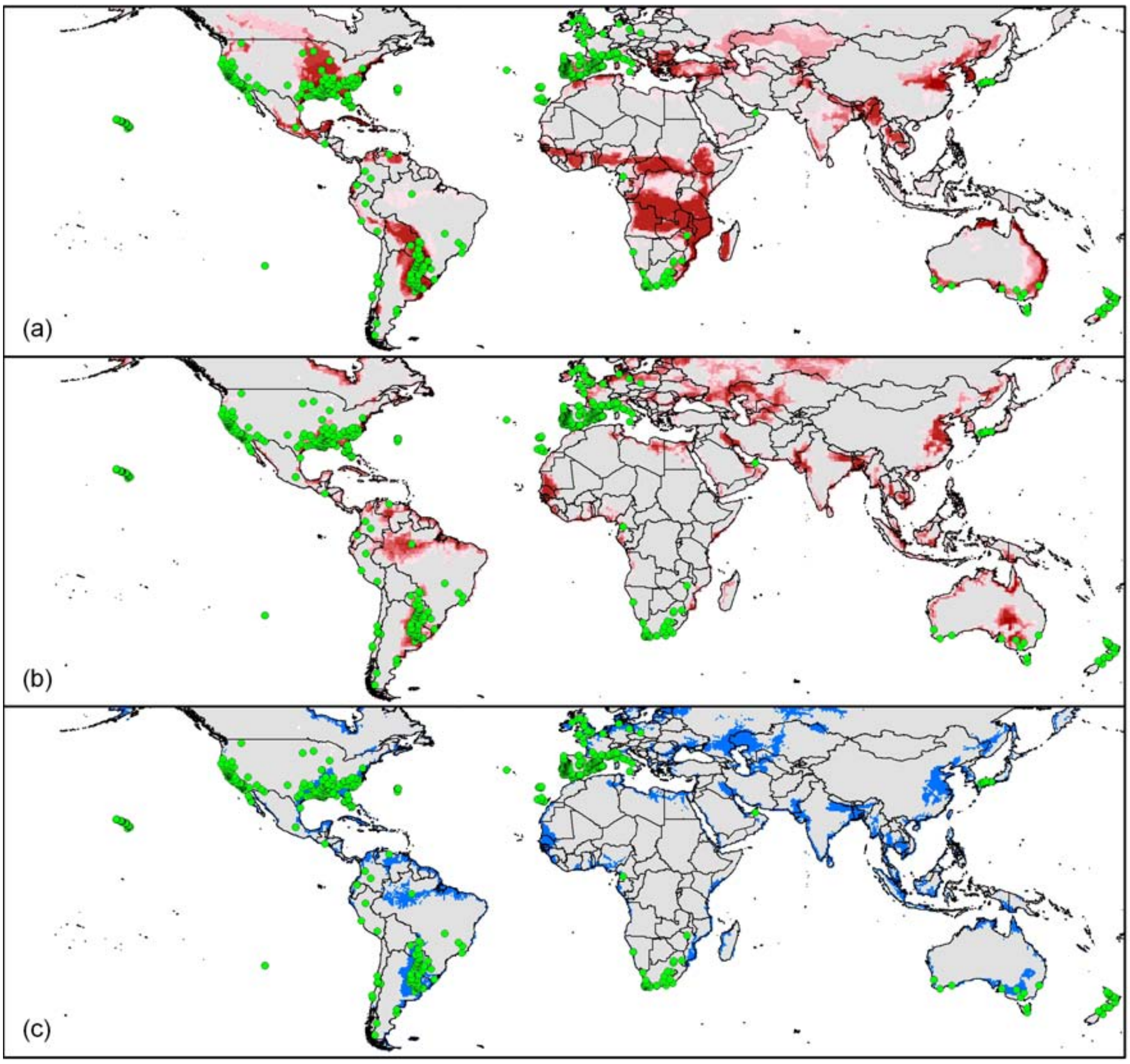

Figure 2 Worldwide predicted potential distribution for the Argentine ant, based on native-range ecological niche models based on: (a) climate data, and (b) NDVI data sets; (c) coincident areas identified in both modeling efforts (in blue). Occurrences of the species in both the native and the invaded range are plotted as dots. Darker shading indicates greater model agreement in predicting potential Argentine ant presence.

Table 1 Summary of statistical tests of model predictions for the whole world and for 2 densely sampled regions, based on 2 sets of environmental data: climate and NDVI. Tests were performed for areas predicted by $\geq$90% of best-subsets models (1st line) and by any of 100 best-subsets models (2nd line). North America and Western Europe test areas were analyzed only for areas within 500 km of test occurrence data.

	Climate data set							
	Prop. area	Test N	Obs. correct	Obs. incorrect	Exp. correct	Exp. incorrect	X^2	*P*
World	0.07	791	593	198	258	533	643.9	$<10^{-100}$
			258	533	54	737	830.3	$<10^{-100}$
N America	0.23	266	200	66	141	125	52.8	$<10^{-12}$
			101	165	62	204	32.3	$<10^{-7}$
W Europe	0.05	330	276	54	144	186	213.4	$<10^{-47}$
			83	247	16	314	305.6	$<10^{-67}$
	NDVI data set							
	Prop. area	Test N	Obs. correct	Obs. incorrect	Exp. correct	Exp. incorrect	X^2	*P*
World	0.02	1021	526	495	59	962	3956.1	$<10^{-100}$
			262	459	19	1002	3245.0	$<10^{-100}$
N America	0.06	295	176	119	41	254	522.2	$<10^{-100}$
			94	201	18	277	346.1	$<10^{-77}$
W Europe	0.07	458	237	221	82	376	357.8	$<10^{-79}$
			102	356	30	428	181.1	$<10^{-40}$

Validations of invaded-range predictions in densely-sampled regions (United States and western Europe) and worldwide were uniformly significantly better than random expectations (χ^2 tests, all $P < 10^{-7}$; Table 1). Hence, this set of tests indicates that the worldwide projection of the native-range ecological niche model had considerable predictive power for distributional phenomena in this species as an invasive species. Based on present knowledge of the species, predicted areas in northern latitudes (principally in NDVI predictions, and apparently caused by inclusion of topographic variables, given tests with and without this suite of variables) are not reliable. Likewise, areas of underprediction (i.e., where predictions are negative but the species is known to be present) are minor, and correspond to urban localities where the species' presence may be made possible by the subsidy of human presence. Although predictions in some areas underestimated or overestimated the species' invasive potential, their ability to identify key distributional areas was clearly much better than that of random models.

Future potential distributions

For development of future-climate predictions, we performed the jackknife manipulation to reduce the dimensionality of models: coverages retained for analysis were minimum and mean annual temperature, precipitation, slope, and flow direction (inclusion of each was negatively associated with omission error). Given the coarser sample-size considerations resulting from the coarser resolution of the environmental data sets for future climates, we could validate these present-day native-range predictions only using χ^2 tests—models were significantly more accurate than random models ($P < 10^{-3}$). Projecting these models onto the four general circulation model scenarios of future climates, *L. humile* was generally predicted to experience worsening conditions in the Tropics, but improving conditions at higher latitudes (Figure 3). Overall, the spatial extent of the spatial projection of the species' ecological niche is expected to undergo a moderate (11-15%) reduction under all four future scenarios (Figure3).

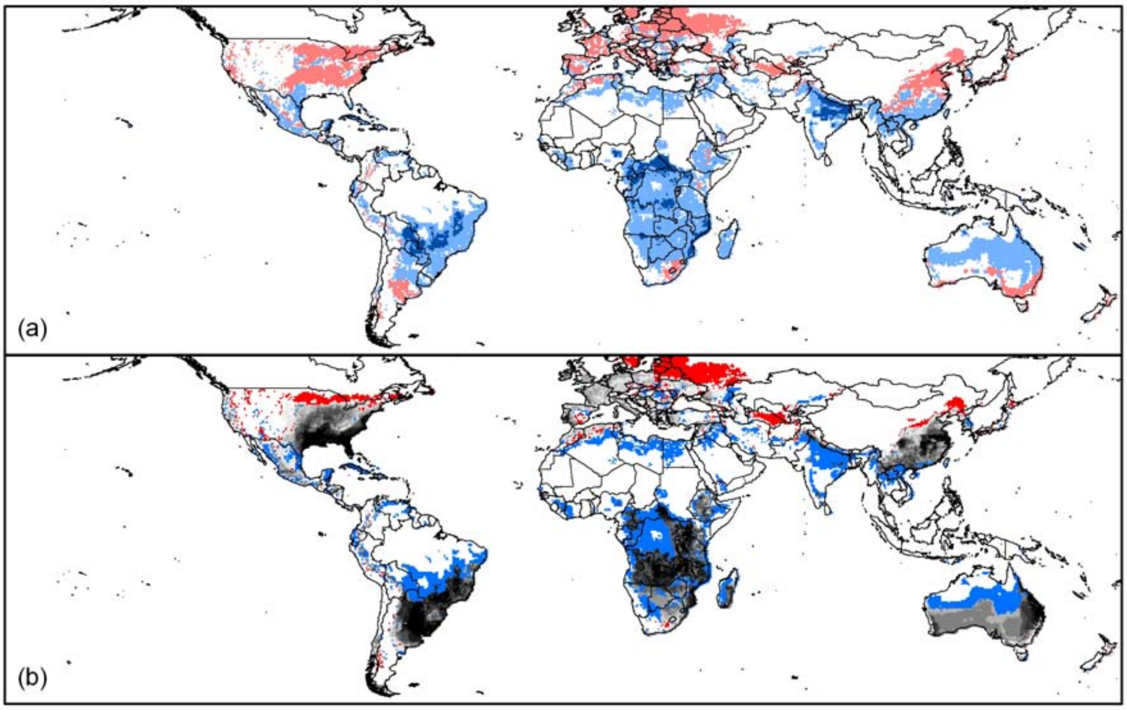

Figure 3 Worldwide predicted changes in potential distributional area for the Argentine ant between present and 2050. (a) Difference maps (future suitability values minus present suitability values), showing expected changes in climatic suitability for Argentine ants: red shades indicate areas predicted to improve for Argentine ants, whereas blue shading indicates areas predicted to worsen for the species. (b) Areas predicted to become newly habitable or non-habitable for the Argentine ant: the grey scale indicates present-day potential presence (darker shades greater confidence), red indicates areas predicted to become habitable but not presently habitable, and blue indicates areas presently habitable but predicted to become non-habitable in the future. Maps represent the average predictions of 4 scenarios of global climate change: HadCM3A2, HadCM3B2, CGCM2A2, and CGCM2B2.

Discussion

The accuracy of models developed for the potential distributions of species depends on available sample sizes for model-building (Stockwell and Peterson 2002), and on the complexity of the environmental data sets (Peterson and Cohoon 1999). In this case, excellent predictive accuracy was achieved with models based on 5-7 coverages. Differences in the final environmental coverages retained for each model depend on the nature of the ecological niche approach, wherein the combination of ecological parameters determines the potential distribution of the species instead of each environmental parameter alone. This result is consistent with previous studies (Peterson and Cohoon 1999, Stockwell and Peterson 2002). In general, at least for this species, these results suggest that 67 native-range localities were quite sufficient for modeling and predicting distributional phenomena.

Differences between the predictions developed for the native range reflect the differences between the two environmental data sets (climate vs. NDVI) used for modeling. Predictions based on NDVI data are more restricted spatially than predictions based on climate data, likely reflecting the greater detail in such remotely sensed data. Studies of factors governing Argentine ant invasions (Way et al. 1997, Holway 1998, Human et al. 1998, Paiva et al. 1998, Suarez et al. 2001, Holway et al. 2002b) suggest that both climatic and topographic constraints are important in determining its distribution, but that other factors such as vegetation type, soil type, or perturbation of habitat may also be limiting (Paiva et al. 1998). For this reason and according to our results, we take both sets of predictions into account, and consider areas predicted by both models as the likely native distribution of the Argentine ant (Figure 1c).

In northern Argentina and southern Paraguay, *Linepithema humile* is almost always found along major river systems. They can be found in both disturbed and undisturbed areas, with highest densities along floodplains, in riparian areas, and on riverine beaches (Wild 2004). Our models nevertheless suggest the possibility of a broader distribution in its native range than is presently appreciated. Invaded-range predictions also indicate a broader potential distribution than is currently appreciated. Despite its widespread occurrence, many areas still remain vulnerable to invasion by Argentine ants (if they are not already there but undetected). Especially important are areas where few or no records of Argentine ants are known, particularly northern South America and the Caribbean, parts of the Mediterranean, eastern Europe, tropical coastal Africa, Madagascar, Southeast Asia, India, China, northern Australia and many oceanic islands. These predictions coincide with those by S. Hartley *et al.* (pers. comm.) on a coarse scale.

Our identification of new potential sites of invasion demonstrates the utility of our approach as a tool for prevention of new infestations. Given that efforts to eradicate Argentine ants have almost no success once the species is established (Krushelnycky and Reimer 1998), these areas should be vigilant in preventing the introduction of this species via improved quarantine measures or other means. That predicted potential areas exceed actual distributional areas can result from remaining invasive potential, but also from insufficient sampling, recent invasion, or the existence of additional factors that restrict distributions (e.g. existence of allopatric sister species, interspecific competition, previous extinctions, and limited dispersal abilities; (Peterson 2003)). Specifically, for the native range, areas lacking occurrence data can be likely explained by insufficient survey, or possibly to the presence of related species (Tsutsui et al. 2001, Wild 2004) that could represent potential competitors. For these reasons, a species' potential distribution is generally more extensive than its actual distribution (Peterson et al. 2002b, Peterson 2003). A better understanding of how these processes determine Argentine ant distributions would permit a better understanding of details of the distributional ecology of the species. Moreover, anthropogenic factors may also result in a lack of concordance between actual and predicted distributions of invasive species. For example, the success of Argentine ants in California has been tied to increased moisture levels associated with urban and agricultural runoff (Holway et al. 2002b). Modeling approaches, such as those employed here, do not take into account human-related disturbances and in that way can underestimate a species' potential distribution. Approaches that incorporate land use, water supplementation, or other anthropogenic factors may not only have increased predictive power, but also provide may insight to specific factors responsible for detailed distributional phenomena.

In relation to global warming, our predictions suggest a general reduction of potential distribution areas for *L. humile*, particularly in the Tropics. However, some higher latitude areas are predicted to become more suitable for invasion (East Asia, northeastern United States, broader areas around Mediterranean and Caspian Seas, southern Africa, and southern Australia). Modeling influences of global climate change on a species' potential distribution presents some initial limitations: predicted distributions of species are based on climatic envelopes, not taking into account the influence of dispersal, source-sink dynamics, and species interactions (Davis et al. 1998, Peterson et al. 2001). In spite of these limitations and the lack of knowledge on how *L. humile* responds to climate change (adaptation to the new ecological characteristics, dispersal to track its ecological niche, etc.), our analyses represent a first step towards understanding influences of global climate change on *L. humile*'s potential distribution, and indeed one of the very first applications of ecological niche modeling techniques to the challenge of anticipating changes in invasive potential of species. More generally, given that changes in species' distributions alter global biodiversity (Chapin et al. 2000, Sala et al. 2000), species' invasion appears as a primary threat resulting from global climate change. In this sense, studies identifying potential new areas for invaders should be seriously considered in polices of introduction prevention.

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Chapter 3

Niche Differentiation and Fine-scale Projections for Argentine Ants based on Remotely Sensed Data

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CHAPTER 3

Niche Differentiation and Fine-scale Projections for Argentine Ants based on Remotely Sensed Data[7]

Abstract

Modeling ecological niches of species is a promising approach for predicting the geographic potential of invasive species in new environments. Argentine ants (*Linepithema humile*) rank among the most successful invasive species: native to South America, they have invaded broad areas worldwide. Despite their widespread success, little is known about what makes an area susceptible -or not- to invasion. Here, we use a genetic algorithm approach to ecological niche modeling based on high-resolution remote-sensing data to examine the roles of niche similarity and difference in predicting invasions by this species. Our comparisons support a picture of general conservatism of the species' ecological characteristics, in spite of distinct geographic and community contexts.

Introduction

Biological invasions are a significant consequence of, and component of, human-caused global change (Vitousek et al. 1997). Although biotic invasions are neither new nor an exclusively anthropogenic phenomenon, the number and extent of non-native species is increasing at a rapid rate as a consequence of increased human mobility (Levine and D'Antonio 2003, Drake and Lodge 2004). These human-caused invasions alter global environments, generating important environmental, societal, and economic impacts (Mack et al. 2000); indeed, consequences of these changes are so important that new tools are needed to facilitate prevention of invasions and control of non-native species. By this token, approaches for modeling geographic distributions of species have seen increasing application in recent years (Guisan and Zimmermann 2000), and their extension to species' invasions (Peterson 2003, Thuiller et al. 2005) represents promising new possibilities.

The Argentine ant (*Linepithema humile*) is one of the five ant species ranking among the world's 100 worst invaders (http://www.issg.org). Native to northern Argentina, southern Brazil, Uruguay, and Paraguay (Tsutsui et al. 2001, Wild 2004), it is now established in many parts of the world owing to human-mediated transport (Suarez et al. 2001, Roura-Pascual et al. 2004). Introduced populations of this species can cause severe ecological and economic effects (Holway et al. 2002a).

As with most invasive species, multiple factors contribute to success of Argentine ant populations in introduced ranges. For example, Argentine ants have been introduced without their co-evolved natural enemies, and the ant communities they invade tend to be depauperate relative to the species-rich ant fauna of southern South America (Suarez et al. 1999, Holway et al. 2002a, Heller 2004). Moreover, Argentine ants appear to be better competitors than the native species they generally displace (Human and Gordon 1997, Holway 1999). Recent studies suggest that

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[7] See Chapter 1and 6 for a posteriori nuances to this chapter according to recently published studies. We preferred to maintain the text of this chapter as it will appear published.

phenotypic and genetic changes occurring during or after introductions may influence invasive success (Ross et al. 1996, Tsutsui et al. 2000, Holway and Suarez 2004). While these studies focus primarily on behavioral differences or changes in colony structure, changes in physiology or tolerance to environmental conditions could also affect the extent to which invasive species can invade new environments. The consequences of these changes for the success of Argentine ants in invading new environments remain unknown; clearly, further detailed comparisons between native and introduced populations are necessary.

In this study, we examine differences in ecological niche characteristics of Argentine ants between native and introduced populations to understand ecological changes that may or may not have occurred, and to predict the potential for future invasions. Species' geographic distributions are influenced by their ecological niches--the set of environmental conditions within which a species can maintain populations without immigrational subsidy (Grinnell 1917). Although several studies (Huntley et al. 1989, Peterson et al. 1999, Martínez-Meyer et al. 2004) have observed general conservatism in species' ecological niches on evolutionary time scales, few studies have assessed the stability of niche characteristics when populations are transplanted to another continent presenting a distinct biotic community context (Fitzpatrick and Weltzin 2005). Introduced species tend to establish populations in areas matching the environmental conditions of their native distributional areas (niche stability or niche conservatism) (Peterson 2003). Nonetheless, it is possible that shifting interactions given biotic community differences between distributional areas, or evolutionary changes post-introduction may produce shifts in ecological niches characteristics (niche differentiation/evolution) (Peterson and Holt 2003, Wiens and Graham 2005).

We build on our previous studies of potential geographic distributions of *Linepithema humile* at global scales for present and future climate scenarios (Roura-Pascual et al. 2004)[8], as well as on work at local scales by Hartley and Lester (2003), by comparing native and invaded-range ecological niches of this species at high resolution. Our approach permits analysis of ecological requirements for successful invasion by Argentine ants at regional scales, providing an opportunity to test whether differences in invasion success across introduced populations correlate with recent evolutionary changes. Finally, this study tests the utility of remote-sensing data for predicting the geographic potential of invasive species.

Methods

A tested approach for estimating species' ecological niches is the Genetic Algorithm for Rule-set Prediction (GARP; Stockwell and Peters 1999, Anderson et al. 2003, Peterson 2003). GARP is an evolutionary-computing approach that searches for non-random associations between occurrences of species (georeferenced localities in geographic coordinates) and environmental variables (i.e., digital maps of relevant ecological parameters). Inspired by models of genetic evolution, GARP models are composed of sets of rules that were "evolved" through iterative processes of rule selection, evaluation, testing, and incorporation or rejection.

Input data.-- Georeferenced localities on which we based our models were extracted from museum specimen locality records and personal collections, scientific literature, and field surveys (see Annexes 1 and 2, although some localities were omitted due to changes in the resolution of environmental data). Overall, we used 64 occurrence points from the native distributional area, and 341, 280, and 9 points from invaded areas in the Iberian Peninsula, North America, and Japan, respectively.

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[8] See note 3 in page 34

The environmental data sets included 30 digital maps (”coverages”) summarizing aspects of topography (elevation, topographic index, slope, aspect, flow direction and flow accumulation, from the US Geological Survey’s Hydro-1K data set,[9] spatial resolution 1 x 1 km) and 16-day composite remotely-sensed data layers (one composite per month during 2003 of the Normalized Difference Vegetation Index (NDVI) and the Enhanced Vegetation Index (EVI), from the spaceborne NASA-MODIS/Terra optical imager at a spatial resolution of 500 x 500 m[10]; Justice et al. (1998). Differences in summer-winter timing between Northern and Southern hemispheres were resolved by shifting Southern Hemisphere monthly data by 6 months, and thus aligning northern and austral summers and winters appropriately. The two vegetation indices are derived reflectance values measured in the visible and near-infrared domains, and are complementary: while NDVI is more sensitive to chlorophyll content, EVI (L=1; $C1$=6; and $C2$=7.5 as equation coefficients) is more responsive to canopy structural variations (Huete et al. 2002). Thus, these indices act as surrogates for land cover variables, and as such are closely related to climatic dynamics (Egbert et al. 2002). Climatic data were not taken into account directly because of the lack of such data at appropriately fine resolution for all areas. All geographic data were resampled to 1 km resolution to facilitate analysis across broad spatial extents.

The GARP algorithm.-- GARP maps occurrence data into a regular grid at the same scale and extent as the environmental data, allowing only one occurrence to be selected from each pixel. First, grids cells holding known occurrences are divided into data input into the genetic algorithm for model development and an independent data set (“extrinsic testing data”) for evaluation of model quality at user-specified proportions (here, 50% and 50%, respectively). Then, the input data are resampled with replacement to create a set of 1250 presence points; an equal number of points is also resampled randomly from the set of grid pixels at which the species has not been recorded (pseudo-absences). The input data are further subdivided into training data (for rule development), and intrinsic testing data (for evaluation of rule predictivity). Changes in predictive accuracy from one iteration to the next are used to evaluate whether particular rules should be incorporated into the model or not, and the algorithm runs either 1000 iterations or until convergence. The final ecological niche model rule-set is then projected onto the digital maps that are the environmental data sets input into the algorithm to identify areas fitting the model parameters, a hypothesis of the potential geographic distribution of the species.

Subsequently, once the final rule-set (or individual model) is developed, predictive accuracy of each model is also evaluated based on the extrinsic testing data. Spatial predictions of presence and absence can hold two types of error: omission (areas of known presence predicted absent) and commission (areas of known absence predicted present), which can be summarized in a measure of predictive accuracy as the percentage of points correctly predicted as present or absent (the correct classification rate of Fielding and Bell (1997)).

Given the stochastic nature of GARP (both via sampling of occurrence data and the genetic algorithm itself), GARP produces distinct results for alternate runs based on the same input data, representing alternative solutions to the computational challenge. Following recently proposed best-practices approaches (Anderson et al. 2003), we developed 100 replicates of each model (previous tests with 1000 replicates showed that more models do not improve the final best-subset models, but do meet with computational limitations); of these, we retained the 20 models with lowest omission error, and then discarded the 10 models of these 20 that presented the most extreme values of area predicted present (the “commission error index” of Anderson et al.

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[9] http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html

[10] http://edcimswww.cr.usgs.gov/pub/imswelcome/

(2003)). These “best subset” models were summed to produce final predictions of potential distributions.

Models were validated using the Receiver Operating Characteristic (ROC) analysis, which evaluates model performance independently of arbitrary thresholds at which presence might be accepted (Fielding and Bell 1997, Manel et al. 2001, Pearce and Boyce 2006). ROC assesses model performance by plotting sensitivity (proportion of presence points correctly predicted) vs. 1-specificity (proportion of absences correctly predicted) across all possible thresholds. Because true absences were not available for all areas, pseudoabsences (any pixel without confirmed presence) were employed as surrogates (Wiley et al. 2003, McNyset 2005). Given computer limitations, the ROC analysis was performed on a randomly selected subset (5%) of the overall predicted areas. Good model performance is characterized by large areas under this curve (AUC; maximizing sensitivity for low values of 1-specificity): AUC values of 0.5 indicate models with no accuracy, while AUC values of 1.0 indicate high accuracy. A z-statistic was used to compare observed AUC with the random AUC (following formulas in Hanley and McNeil (1982)), or between AUCs for two independent analyses (following formulas in Hanley and McNeil (1983)); if $z > 1.96$, then the probability is < 0.05 that the observed difference would be expected at random.

Modeling approach of this study.-- The overall approach used to compare ecological niches of Argentine ants in different regions (native distribution, Iberian Peninsula, North America, and Japan) consisted of three steps. This first step (step 1) is designed to optimize the environmental data sets for predicting the species’ ecological niche in succeeding steps. Hence, we used a cross-validation analysis between two regions: models based on occurrences from the native range were projected onto the Iberian Peninsula and vice versa, and model performance was tested using ROC on the projected region using the occurrence data set aside from model development. Seven predictions were developed for each occurrence data set, representing all combinations of suites of environmental data sets: topography (H), NDVI (N), and EVI (E) combined for analysis as H, N, E, HN, HE, NE, and HNE. Based on results of these cross-validation analyses, taking higher test AUC scores as an indication of a better environmental data set for characterizing that species’ ecological niche, we chose a suite of environmental data sets for further analyses.

Second (step 2), we tested the suitability of each occurrence data set within each region, when possible given sample sizes (i.e., excluding Japan). Occurrence data were divided into two subsets for training and testing model performance in geographically separate areas, as follows. Native-range occurrences were divided depending on their location on a 2 º x 2º checkerboard (44 occurrences for subset 1, and 23 occurrences for subset 2); Iberian Peninsula were divided into eastern (<2º W longitude, 206 occurrences) and western (>6º W longitude, 176 occurrences); and North American occurrences were divided into eastern (<100º W longitude, 123 occurrences) and western (>108º W longitude, 156 occurrences). We validated within-region model predictivity using one of the subsets listed above to predict the other, and vice versa, and evaluated model performance using ROC. As this test forces the model to predict into areas from which no occurrence points were used in training the model, high AUC-values indicate successful ability of models in predicting into broadly unsampled regions.

Finally (step 3), we performed an overall cross-prediction analysis, building models and predicting between all regions for assessing the strength of niche differences. Each regional occurrence data set (native range, Iberian Peninsula, North America, Japan) was modeled using GARP, and the resulting ecological niche model (ENM) projected onto each other regional data set. ENM performance in predicting ‘other’ regions was evaluated using the ROC procedure described above. High AUC values indicate that model predictions are better than random expectations, i.e. how well the model generated in one region correctly predicted the occurrence data of another region; because the ROC approach simply concludes that a prediction is (or is not) better than random, we also present basic statistics on model performance (i.e., omission, commission).

To visualize ecological niche differences between different models developed, we used principal components analysis to reduce the 30 initial input variables to the first two principal components, which explained the bulk of variance in ecological space. Given limitations on computer memory, we subsampled grids randomly at a density of 1:500, and used this reduced suite of grid squares for visualizations, in which we related areas of modeled presence to overall availability of environmental conditions.

Results

Selecting environmental data sets

ROC tests performed on projections from the native-based models to the Iberian Peninsula region and vice versa, yielded significant z-values ($P < 0.001$) for all combinations of environmental data sets (H, N, E, NE, HN, HE, and HNE), indicating substantial capacity for all environmental data sets in predicting the species' distribution. Projections from the native-based model to the Iberian Peninsula presented AUCs ranging from 0.53 for E alone to 0.76 for HE. Still high values of AUC, indicating useful predictions, were obtained based on all environmental variables (0.73 for HNE) or with topography alone (0.75 for H). Similarly, projections from the Iberian Peninsula to the native range give AUCs between 0.59 (H) and 0.71 (N). Although the somewhat lower AUCs suggest lower accuracy than native-range models, all models appear capable of predicting the species' range. Overall, according to the ROC tests and visual comparisons among native-range and Iberian Peninsula predictions (not shown), our interpretation is that the combination of topographic information with both vegetation indices (HNE) represents the optimal assemblage of environmental information for predicting Argentine ant distributions.

Within-region predictivity data set

The tests of occurrence predictivity within three regions (native range, Iberian Peninsula, North America) using the subsets described in the Methods indicated quite powerful predictive ability. In fact, using the HNE environmental data sets, all 6 reciprocal predictions were statistically significant based on the ROC tests ($P < 0.001$). The native-range models showed the lowest AUCs[11] ($AUC_{subset1}=0.62±0.06$, and $AUC_{subset2}=0.73±0.05$) in relation to the Iberian Peninsula ($AUC_{east}=0.75±0.02$ and $AUC_{west}=0.76±0.02$) and North America ($AUC_{east}=0.90±0.02$ and $AUC_{west}=0.77±0.02$), probably reflecting lower sample sizes. Omission rates (i.e., failure to predict known occurrences) were low (Table 1), suggesting that the ENMs were successfully predicting extents of occurrences in each region. Overall, the results of these tests indicate significant predictive power for modeling Argentine ant distributions in a variety of geographic contexts.

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[11] AUC subindices indicate the subset used to build the models.

Niche comparisons among regions

All cross-predictions among distributional regions (native range, Iberian Peninsula, North America, Japan) were statistically significant in ROC tests ($P < 0.01$; Table 1). As such, a general result of these analyses is that we find no evidence that ecological niches have either evolved or have been modified by different community contexts in the species' colonization of areas worldwide over the last century (Peterson et al. 1999). However, some differences do appear between the actual predictions of different regional models (Figure 1).

Native-range models accurately predicted known distributions of Argentine ants in each invaded region (Table 1). However, these models also suggest additional areas in which Argentine ants are not known to occur--ostensibly areas of potential future invasion. For example, projections for the Iberian Peninsula successfully predicted species' presence along southern and western coastlines, but suggested the potential for expansion into the interior of the Iberian Peninsula. Similarly, these models correctly predicted known Argentine ant distributional areas along the southeastern and western coasts of North America, but again highlighted interior areas as also suitable for the species. On the other hand, invaded-range models provided results somewhat different

Table 1 Statistical results of cross-prediction comparisons among distributional regions for the Argentine ant. Occurrence data from each region were used to develop ecological niche models (first column), which were then projected onto each other region (side headings of the first column delineating sections) for testing model accuracy using Receiver Operating Characteristic (ROC) analysis. For each predicted region two analysis are presented: (1) general statistics as area under the curve (AUC) and its standard error, omission (percentage of occurrence data incorrectly predicted as absent), and commission (percentage of area predicted present) at two different thresholds (areas predicted by >90% of best-subset models and by any of 10 best-subset models respectively); and (2) significance in the *z* test comparing the AUCs (three right-hand columns) among models. Asterisks indicate the significance of *z* tests: * for $P<0.05$, ** for $P<0.01$, and *** for $P<0.001$. Sample sizes represent the number of Argentine ant localities used for developing the models. All models were developed using the combined topography, normalized difference vegetation index (NDVI), and the enhanced vegetation index (EVI) environmental data set (HNE).

		Omission		Commission		AUCs'comparisons		
Model	AUC	>90% best	10 best	>90% best	10 best	Iberian	N Amer	Japan
Native area (*n*=64)								
Native	0.7512±0.0354***	10.9	0	50.8	79.3	***	***	**
Iberian	0.6125±0.0375***	40.6	3.1	41.7	99.0		ns	ns
N Amer	0.6185±0.0375***	15.6	1.6	67.0	93.4			ns
Japan	0.6098±0.0375***	98.4	75.0	0	3.5			
Iberian Peninsula (*n*=341)								
Native	0.7564±0.0153***	44.3	9.7	9.0	74.8	ns	***	***
Iberian	0.8308±0.0137***	14.7	3.2	26.9	53.1		***	***
N Amer	0.5927±0.0162***	10.0	2.1	76.2	96.3			ns
Japan	0.5618±0.0161***	94.1	64.8	0.7	25.1			
North America (*n*=280)								
Native	0.7842±0.0163***	40.0	7.9	8.2	82.8	ns	ns	***
Iberian	0.8371±0.0149***	43.6	9.3	6.9	51.4		*	***
N Amer	0.8025±0.0159***	5.0	0	40.6	77.6			***
Japan	0.6356±0.0179***	93.2	52.9	1.2	21.5			
Japan (*n*=9)								
Native	0.7841±0.0909***	44.4	11.1	15.9	43.1	ns	ns	ns
Iberian	0.6579±0.0996**	44.4	11.1	11.8	79.8		ns	ns
N Amer	0.7316±0.0960***	22.2	0	34.4	79.8			ns
Japan	0.9880±0.0256***	55.6	0	0.9	8.4			

from the native-range models. For example, models based on occurrences in the Iberian Peninsula predicted potential distributional areas on the coast and along important rivers in the Iberian Peninsula, perhaps reflecting some degree of coastal bias in the occurrence data available from that region. North American and Japanese models predicted new potential areas for invasion where Argentine ants are not presently documented (e.g., northern USA and Japan, interior areas along major rivers).

Comparing AUCs of native-range-based models with those of invaded-based models projected to the native area, AUCs are significantly higher in models based on invaded areas ($P < 0.01$), suggesting that regional models vary somewhat in how they characterized the ecological niche of the species. Comparisons between the native- and invaded-based models for given regions also exhibit differences, particularly for the native area, whereas native- and invaded-based models for the Iberian Peninsula, North America and Japan are not significantly different (Table 1). North America-based models predicted the broadest potential distributions in all areas, indeed somewhat overpredicting the actual distribution of the species. Finally, Japan-based models presented less intense and less extensive predictions in other regions, probably reflecting small sample sizes across an ecologically restricted landscape or non-equilibrium distribution in Japan.

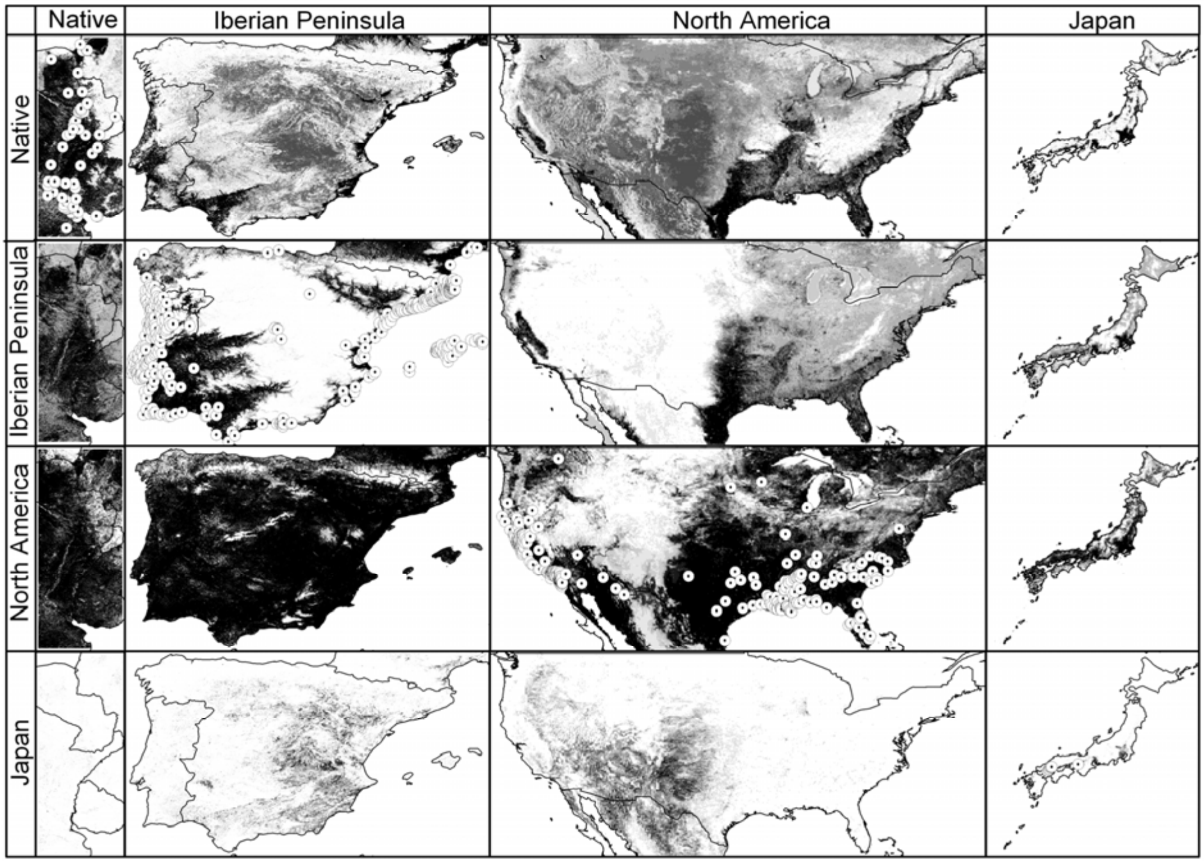

Figure 1 Predicted distribution of the Argentine ant among the native range, Iberian Peninsula, North America, and Japan. Regions used to develop models are in each row, and columns indicate the region to which the model was projected. All models were developed using the combined topography, normalized difference vegetation index (NDVI), and the enhanced vegetation index (EVI) environmental data set (HNE). Greater model agreement in predicting potential occurrence is indicated in darker shades, and dotted circles indicate occurrence data used to build models.

These differences between model predictions may result from environmental differences among regions, differences in invasion biology, or differences in sampling schemes. The species' ecological niche as modeled in each area and projected to each other area can be represented in bivariate plots of the principal components summarizing environmental space, which explained 61.2% of total variation in environmental parameters in the PCA analysis. PC1 (49.6% variation) was correlated positively with elevation (0.585), and negatively with NDVI and EVI values (ranging from -0.653 to -0.892); PC2 (11.6% variation), on the other hand, was related positively with EVI of August and July (0.555 and 0.534 respectively), and negatively with NDVI of February and January (-0.593 and -0.523 respectively). In general, Argentine ant ecological niches as reconstructed in its native range, the Iberian Peninsula, and North America were quite similar (Figure 2), but that reconstructed based on Japanese occurrences was considerably more restricted, again likely reflecting either a still-small distributional area there or limited sampling compared with other areas. In general, comparing conditions available across areas, differences observed are most likely artifacts of sampling or environmental differences among areas, and not real differences in the species' ecological niche.

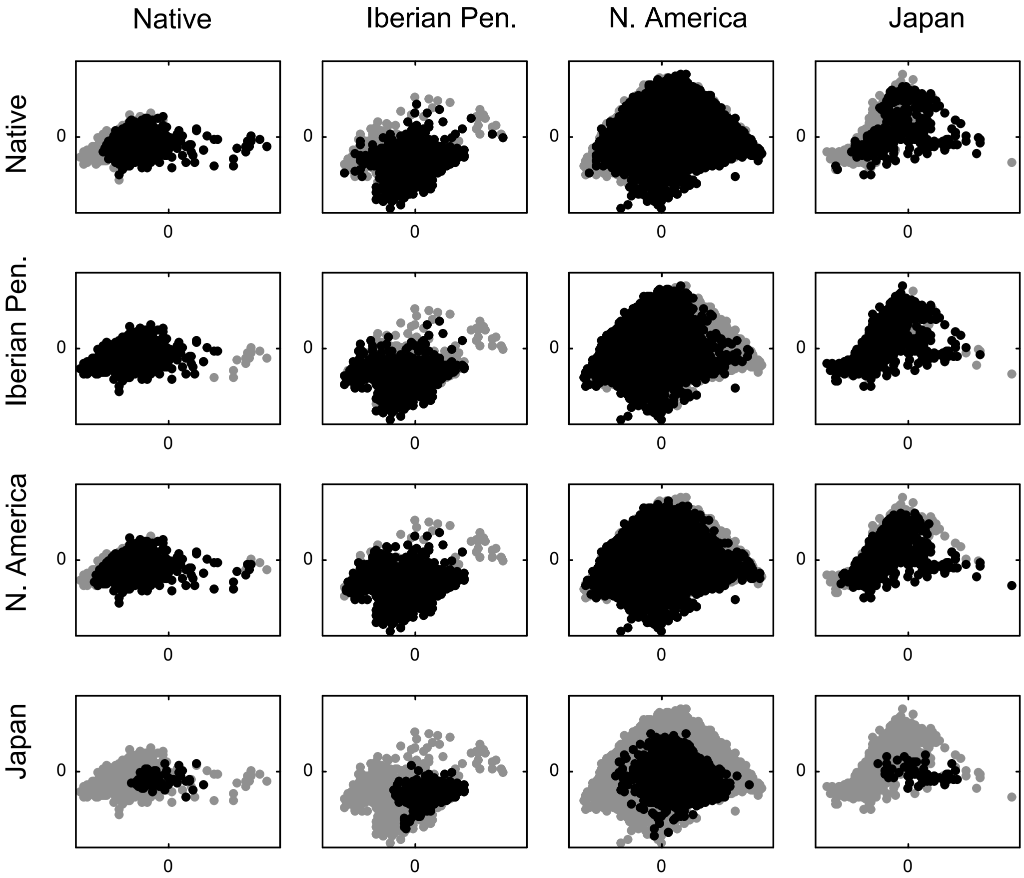

Figure 2. Visualizations of Argentine ant niche models in ecological space, in the form of a bivariate plot of principal components 1 and 2 (PC1 and PC2), which summarize overall variation patterns in the 30 original dimensions in which we studied the species' niche. Black points indicate predicted presence, whereas grey points indicate environmental conditions present in the area but not predicted as habitable for the species. Rows indicate the region used for building models, and columns indicate the region to which models were projected.

Discussion

This study develops and compares ecological niche characteristics of Argentine ants on the species' native range and in three invaded areas. A previous study (Roura-Pascual et al. 2004) examined the species' global potential for spread based on its native-range ecological niche, and suggested that the overall approach held promise for modeling this species' potential geographic distribution. This study confirms and expands the previous results by examining differences between ecological niches as reconstructed from points on native and invaded ranges at much finer resolution and with more analytical detail.

Overall, tests assessing robustness and adequacy of the environmental and occurrence data sets employed indicated that they were sufficient for comparing native- and invaded-range ecological niches of Argentine ants. Statistical tests and visual inspections of models generated using all possible combinations of environmental data sets (step 1) suggest that those models based on vegetation indices alone predicted broader potential distributions than models including only topographic information. Although models based on NDVI and EVI together seem possibly overfit, we preferred to use both indices because they presented slight differences in their predictions, and predictions from models generated using all available environmental data (HNE) were highly accurate in the ROC tests. This result is consistent with previous studies (Holway 1998, Paiva et al. 1998, Holway et al. 2002b) that suggest that topographic, climatic, and habitat data are all important factors governing Argentine ant distributions.

Regarding sample sizes, our results suggest that ~60 occurrence points would be sufficient to achieve maximum predictive accuracy. Japan was excluded from these within-region analyses because of the small sample size available (Stockwell and Peterson 2002b). However, Japan-based models were kept in the cross-prediction analyses (step 3), so AUC values for predictions of Japanese distributional region are potentially misleading, given a decided lack of statistical power (*n* = 9 occurrences only).

The results of the cross-prediction analysis (step 3) suggest that ecological niche characteristics do not differ markedly between native and invaded ranges at the spatial and temporal scale of our analysis. As such, these results complement those of previous studies (Peterson 2003) in demonstrating general conservatism of species' ecological niches. Within this general result of ecological niche stability among Argentine ant populations, however, we did observe some region-to-region variation in model results (Figure 1 and Table 1). These variations may be the result of vagaries of sampling, limitations of the modeling tools, environmental difference between regions, or subtle differences between ecological niches of regional populations. Some reasons for variation caused by modeling limitations are explored below:

(1) Data-input related errors, such as occurrence data providing an inadequate sampling of environmental conditions, and/or biased or insufficient environmental data, may introduce model-to-model variation. Our occurrence data come principally from museum specimen label data and personal collections (rather than from planned sampling schemes), so sampling biases can occur. This may be problematic if species' presence is recorded from a building (such as greenhouse) where it may persist regardless of environmental conditions (for example, Argentine ant records from the extreme northern USA). GARP controls these biases to some degree by rasterizing (to reduce redundancy due to duplicate or close locations) and balancing sample size in presence and pseudoabsence data sets (Stockwell and Peterson 2002a). Furthermore, numbers of occurrences were clearly sufficient to prepare models, except for Japan, from which we had limited information. Therefore, GARP appears capable of controlling sampling biases in occurrence data, and providing accurate predictions of Argentine ant distributions.

(2) Only a reduced number of environmental variables is available at fine resolutions for ENM development, which limits predictive capacity of models (Peterson and Cohoon 1999). In this sense, the lack of human-related data at fine resolution impedes taking into account anthropogenic influences (e.g., increased water availability from urban and agricultural sources), which may be a better predictor of Argentine ant establishment and spread than climate envelopes in some arid environments (Holway et al. 2002b). We here resolved this environmental data "gap" via use of remote sensing data, which appears to be an excellent surrogate for land cover and climatic data sets in predicting Argentine ant distribution (Egbert et al. 2002).

(3) Models may need to take into account biotic interactions as well. In this study, we took into account only abiotic variables, and omitted effects that other species might have on Argentine ant distribution and ecology. In the native range, natural enemies and a species-rich and highly competitive ant fauna may well limit Argentine ants from occupying all suitable areas (Holway et al. 2002a, Heller 2004); to the extent that this limitation can act in ecological space and adjust the ecological profile of the species, it may influence our results (Case et al. 2005). Similarly, in North America, another highly invasive ant species, *Solenopsis invicta* may reduce the success of Argentine ants (Wilson 1951, Fitzpatrick and Weltzin 2005), although this idea remains to be tested. Nonetheless, given the high predictive ability of our models among regions, these biotic effects are probably limited in their scope and influence.

(4) The pixel resolution of environmental data (1 x 1 km) may also cloud some finer-scale variations in the species' ecological niche that are not detectable at the spatial scale of our analysis (A. Guisan, *personal communication*). Because the influence of each environmental variable in determining the species' niche is scale-dependent, different degrees of ecological niche variation can arise among populations, depending on the spatial resolution of analyses (Wiens 1989). Nevertheless, these possible finer geographical variations in niches do not alter the accuracy of our models for predicting Argentine ant niches at the spatial resolution of our analysis.

(5) Differences in the range of ecological conditions (limits of ecological space) from region to region may further complicate the situation (Peterson and Holt 2003). That is, if different regions differ in the 'universes' of ecological conditions that they present (Figure 2), models built in areas presenting limited conditions may be unable to generalize to areas that are more ecologically diverse. An example of this effect is shown in Japan-based models, which seemed to have difficulty in anticipating the species' potential distribution in other areas.

(6) Dispersal is an important factor that can influence a species' pattern of invasion (Higgins and Richardson 1999, With 2002). Because Argentine ants commonly spread through human-mediated jump dispersal, natural limitations to dispersal such as ecological barriers may not be as relevant and have minor influences on their distribution at the spatial scale of our analysis (Suarez et al. 2001).

(7) Invasion history needs to be taken into account in predicting the species' distribution (Williamson 1996). The Argentine ant 'invasion' is likely not complete, and thus the species may be out of equilibrium in some regions (Holway 1998, Casellas 2004). As such, occurrence information from some invaded regions may be biased or limited geographically and possibly ecologically, simply reflecting that the species has not reached those areas yet. Such could be the situation in Japan and unsampled areas of potential presence in other regions: future studies should be addressed to determine the actual geographic distribution (i.e., areas of both presence and absence of the species) and the degree of spread of Argentine ants across regions.

Alternatively, real ecological niche differences (that is, the species occupies a different ecological space in two areas, although both areas present the full range of conditions) could result from evolutionary or ecological shifts in the characteristics of the species. In some invasive ants, such as the red-imported fire ant (*Solenopsis invicta*), the little fire ant (*Wasmannia auropunctata*), and the Argentine ant, introduced populations are known to differ from native populations in behavior and colony structure (Ross et al. 1996, Holway and Suarez 1999, Tsutsui et al. 2000, Le Breton et al. 2004). For example, in Argentine ants, differences among populations in the degree of unicoloniality (Tsutsui and Suarez 2003, Buczkowski et al. 2004, Heller 2004, Holway and Suarez 2004), the absence of strong competitors and parasites in new environments, and evolutionary adaptation to new environments could influence invasion success and form the basis for ecological differentiation between native and introduced populations. As ecological differences between native-range and invaded-range areas as measured in this study appear minor, we suspect that these phenotypic differences relating to ecological tolerance of abiotic conditions may not be broadly manifested or pervasive at the coarser spatial scales of our analyses.

More generally, this study has demonstrated two important points. (1) We proved the utility of remotely sensed data in predicting potential geographic distributions of invasive species (Peterson 2003). We also (2) found that ecological niche characteristics of Argentine ants are not markedly different among distributional areas, suggesting that ecological, behavioral, and other differences observed in detailed single-site studies are not manifested at broader spatial scales.

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Chapter 4

Niche models for invasive species: Selecting optimal approaches for cross-prediction analysis at regional scales

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CHAPTER 4

Niche models for invasive species: Selecting optimal approaches for cross-prediction analysis at regional scales

Abstract

Invasive species may frequently alter structure of ecological communities in the near future; however, we still lack tools to understand and predict invasion patterns in new introduced areas adequately. The present study addresses: (1) the potential geographic distribution and ecological requirements of the Argentine ant (*Linepithema humile* Mayr) in the Iberian Peninsula via ecological niche modeling, and (2) provide new insights into modeling methodologies using cross-predictive analyses among distributional areas. The species (first recorded in the region in 1894) is now established in most coastal areas and some interior urban settlements in the Iberian Peninsula (SW Europe), creating concern about its full potential geographic distribution. Niche models were developed using 3 modeling techniques: the Genetic Algorithm for Rule-Set Prediction (GARP), the Maximum Entropy method (Maxent), and generalized linear models (GLM). Models for the eastern and western portions of the Iberian Peninsula were built using identical sets of occurrence and environmental data, and projected to the other region to investigate ecological differences in the invasion process. Model performance in predicting Argentine ant geographic distributions was tested using the area under the Receiver Operating Characteristic curve (AUC). Our results indicate some divergence between modeling approaches, with Maxent producing accurate summaries of the species' distribution, but GARP estimating the species' full potential geographic range. GLM models, however, show inappropriate behavior under some circumstances of the cross-prediction analyses. More generally, models predict Iberian coastal areas and major river corridors as highly suitable for Argentine ants, and indicate that western Iberian populations may occupy broader environmental ranges than eastern populations. In general, our results emphasize the importance of studying species invasions at fine spatial scales, and indicate that further improvements are needed to reduce model uncertainty in cross-prediction analyses.

Introduction

Rates of species introductions are increasing as a consequence of human movements (Vitousek et al. 1997). This non-native presence can have numerous negative influences on native communities and ecosystems, causing species loss, food web reorganization, community simplification, etc. (Chapin et al. 2000, Mack et al. 2000). As a consequence, interest is increasing in techniques for modeling species' potential geographic and ecological distributions to anticipate and possibly prevent establishment of non-native species in new areas (Peterson 2003, Thuiller et al. 2005, Drake and Lodge 2006).

A highly successful invasive species is the Argentine ant (*Linepithema humile*), native to the Río de la Plata region in South America (Tsutsui et al. 2001, Wild 2004), and now established in many Mediterranean-type and subtropical areas worldwide (Suarez et al. 2001). Associated with humans, Argentine ants are easily transported far from their points of introduction (Suarez et al. 2001, Ward et al. 2005), from where they can invade natural areas, causing severe ecological and economical impacts (Vega and Rust 2001).

In the Iberian Peninsula, Argentine ants are present along much of the coastal zone, except for the Cantabrian coast, where records are few; a few population are now known from interior localities associated with urban centers (Espadaler and Gómez 2003, Carpintero et al. 2004). First Iberian observations of Argentine ants date to 1894 in Oporto (western Iberian Peninsula) and 1923 (or possibly 1919) in Valencia (eastern Iberian Peninsula). Although several studies have analyzed Argentine ant invasions in the region (Way et al. 1997, Espadaler and Gómez 2003, Carpintero et al. 2005), none has focused on regional-scale ecological requirements of the species in this part of its introduced range.

Species' distribution patterns are eminently scale-dependent, since different ecological processes emerge depending on the spatial scale of analysis (Wiens 1989, Mackey and Lindenmayer 2001, Farina et al. 2005). Distributional patterns of Argentine ants have been studied at both broad (Hartley et al. 2003, Roura-Pascual et al. 2004, Roura-Pascual et al. in press)[12] and local (Hartley and Lester 2003, Krushelnycky et al. 2005) spatial scales. Here, we analyze Argentine ant distribution at regional scales (Iberian Peninsula) to elucidate broad patterns of invasion in different subregions with contrasting colonization histories and ecological characteristics. At least two points of introduction have been detected along the eastern and western sides of the Peninsula (Espadaler and Gómez 2003); now, the eastern supercolony is differentiated from the main supercolony that is spread more broadly in the Peninsula (Giraud et al. 2002). Mediterranean and Atlantic influences could be responsible for differences in invasion patterns within the Iberian Peninsula.

To identify possible dissimilarities in the invasion process, we perform cross-prediction analysis [also termed reciprocal distribution modeling by Fitzpatrick et al. (in press)] between the eastern and western parts of the Iberian Peninsula. Previous studies were suggestive, given that ecological niche models built on restricted data sets can fail to capture the environmental conditions of the entire geographic area. Thuiller et al. (2004) indicated that the main problem with such procedures--projecting an ecological niche model onto areas different from that used to calibrate it--is when models capture only a subsector of species' responses to environmental predictors, producing niche models that are not globally applicable. Owing to limitations of models in such situations, Araújo et al. (2005) pointed out that use of multiple modeling approaches may help to increase agreement between predictions and reality. Hence, here, we apply 3 modeling approaches in cross-prediction analyses of Argentine ants within the Iberian Peninsula--this study aims to provide new insights into modeling practices that use subset geographic areas to calibrate and ecological niche models.

Methods

The overall approach used herein is based on modeling species' ecological niches, here taken as the set of conditions under which a species is able to persist and maintain stable populations without immigrational subsidy (Grinnell 1917, Hutchinson 1957). Niche modeling techniques relate known occurrences (as geographic coordinates) to environmental variables (in the form of digital raster maps of relevant ecological parameters), which provide surrogates for the overall ecological dimensions of the species' ecological niche. Niche models search for non-random associations between occurrences and environmental data, which are then used to identify areas of landscape that fit the ecological requirements of the species (Soberón and Peterson 2005). A limitation, however, is when ecological characteristics of species' present

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[12] See note 3 in page 34

distributions do not reflect their entire ecological potential because they are out of ecological equilibrium. Despite this limitation, niche models based on occurrence data from introduced ranges can potentially indicate new, although not all, areas susceptible to invasion, and can elucidate ecological processes governing invasion processes (Peterson 2003).

Occurrence and environmental datasets.-- We used 350 known occurrence localities for Argentine ants in the Iberian Peninsula extracted from specimens in natural history museums and personal collections, scientific literature, and field surveys [see Annexes 1 and 2, although some localities were omitted due to changes in the resolution of environmental data]. As no systematic survey covered the whole area, absence data were not available for constructing models, although the utility of such data is regardless limited by the nonequilibrium nature of invasive species' distributions.

For the environmental datasets, we used 12 coverages summarizing aspects of topography[13] [mean elevation (herein abbreviated as *alt*), northern aspect (*aspect*)[14], slope (*slope*), flow direction (*flowdir*), and flow accumulation (*flowacc*), derived from the digital elevation model of the Iberian Peninsula, native resolution 200 x 200 m (Ninyerola et al. 2005)]; and climate[13] [annual solar radiation (*raan*), annual mean precipitation (*plan*), annual mean temperatures (*tmnan*), minimum winter mean temperatures (*tminwi*), and maximum summer mean temperatures (*tmaxsu*)[15], from the Digital Climatic Atlas of the Iberian Peninsula, native resolution 200 x 200 m (Ninyerola et al. 2005)]; and remotely sensed data[16] [16-day composites for the Normalized Difference Vegetation Index (*ndvi*) and for the Enhanced Vegetation Index (*evi*) from July 2005 from the NASA-MODIS/Terra data set, native resolution 500 x 500 m (Justice et al. 1998)]. These environmental data were selected according to knowledge of the species' ecology (Holway et al. 2002, Abril 2005, Krushelnycky et al. 2005, Heller et al. 2006, Menke and Holway 2006), and our previous experience with modeling it (Roura-Pascual et al. 2004, Roura-Pascual et al. in press). We used NDVI/EVI 16-day composites from July because this month is that of peak Argentine ant activity. All data were resampled to 600 m spatial resolution for analysis.

Ecological niche modeling techniques.-- Several techniques are available for modeling species' ecological niches using presence-only occurrence data, many of which generate pseudoabsence data from areas from which the species is not known to occur for contrasts during model training. Modes of generation of these pseudoabsence data vary among modeling approaches, and can influence final model predictions (Pearce and Boyce 2006). As such, since one of our objectives was to test suitability of different methodologies, we applied 3 techniques: GARP (Stockwell and Noble 1992, Stockwell and Peters 1999), Maxent (Phillips et al. 2004, Phillips et al. 2006), and GLM (Guisan et al. 2002, Brotons et al. 2004). The following is a brief summary of each, indicating most relevant points for our analysis.

The Genetic Algorithm for Rule-Set Prediction (GARP) is an evolutionary-computing approach that uses different methods (logistic regression, range rules,

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[13] http://opengis.uab.es/wms/iberia/index.htm

[14] Aspect was transformed to a continuous variable by measuring the percentage of 200 x 200m pixels with values of 250-360º and 0-70º within each 600 x 600 m pixel. This transformation was required for developing GLM models, which can not handle categorical data, and summarizes northward-facing tendency of slopes.

[15] Minimum winter mean temperatures were obtained by calculating the mean of December, January, February, and March minimum temperatures; and maximum summer mean temperatures by calculating the mean of May, June, July, August, September, and October maximum temperatures. Months were selected according to known details of Argentine ant activity; the period May-October is when the species is most active, exceeding the summer season according to Abril (2005).

[16] http://edcimswww.cr.usgs.gov

negated range rules, and atomic rules) to develop a rule-set defining the species ecological niche (Stockwell and Noble 1992, Stockwell and Peters 1999), which is projected into geographic space as a binary map (1 indicates presence, 0 indicates absence). This model evolves through an iterative process of rule selection, evaluation, testing and incorporation or rejection, which randomly subsets occurrence data into training and testing data to estimate predictive accuracy of each rule (here 50% and 50%, respectively). Then, input training presence data are resampled randomly with replacement to create a set of 1250 presence points, and an equal number of points is also resampled randomly from the background area where the species has not been recorded (pseudoabsences). Change in predictive accuracy between iterations is used to evaluate whether particular rules should be incorporated into the model; the algorithm runs 1000 iterations or until convergence.

To optimize model performance, we developed 100 replicate models of ecological niche and chose a "best subset" based on error distributions for individual models (Anderson et al. 2003): we selected the 20 models with least omission error, and then retained the 10 of these models with predicted area closest to the median area predicted among these 20 low-omission models. The geographic predictions of these 10 "best" models were summed to provide a summary of potential geographic distribution for Argentine ant.

The Maximum Entropy method (Maxent) is a machine-learning method that uses a precise mathematical formulation to estimate the probability distribution of a species following the principle of maximum entropy, which supposes that no unfounded constraints should be included in the estimation (Phillips et al. 2006). In constructing the probability distribution, Maxent uses different types of environmental features (linear, quadratic, product, and threshold combinations of raw continuous environmental data, as well as categorical environmental data) and a regularization parameter (β) for each feature, which estimates how close the expected value is to the observed value (Phillips et al. 2004). As with GARP, Maxent creates random samples of background pixels (10,000) from the study area as pseudoabsences during modeling. The probability distribution developed is finally projected onto the geographic space; a probability (expressed as a percentage) is assigned to each pixel, which can be interpreted as an index of its environmental suitability.

Generalized Linear Models (GLM) are generalizations of linear regression models that allow for non-linearity and non-constant variance among data. In GLMs, predictor variables (i.e., the environmental data) are combined to generate linear predictors, related to the expected value of the response variable (i.e., probability of presence versus absence of the species) through a link function (Guisan et al. 2002, Rushton et al. 2004). We used a logistic regression approach, and therefore a logit link function, given the binominal character of our response variable. Predictor variables were included in models with linear and quadratic terms. Although GLMs are usually used with presence-absence data, they have been applied to presence-only situations by using pixels randomly selected from areas from which the species is not known (Pearce and Boyce 2006). Herein, we used a random subset of 10,000 pseudoabsences from the overall study area. All GLM models for the Argentine ant were developed using S-Plus version 6.0.

Approach for modeling Argentine ant distribution in the Iberian Peninsula.-- Our approach for comparing invasion patterns in the western and eastern Iberian Peninsula consisted of two steps. (1) We selected optimal environmental data sets for modeling the species' ecological niche, and (2) we performed a cross-prediction analysis between western and eastern areas to elucidate differences and similarities between areas.

To select environmental data (Step 1), we used a cross-validation analysis within the overall Iberian Peninsula, and between western (UTM longitude <184000) and eastern (UTM longitude >637000) areas. First, we created three occurrence data sets: 350 localities from the whole Iberian Peninsula (herein called *Ib*), 175 localities from the western area (*wlb*), and 142 localities from the eastern area (*elb*) respectively. Each occurrence subset was again subdivided into training (80%) and testing (20%) data for calibrating and testing the accuracy of models respectively. We developed 25 models for each occurrence data set and modeling approach: 1 including all environmental variables, 12 eliminating one variable at a time, and 12 including only one variable at a time.

Final whole Iberian Peninsula-based models were tested using independent occurrence data from the overall Iberian Peninsula set aside from model development. Eastern- and western-based models were each tested twice: first in the area used to calibrate the models using independent occurrences, and second in the other area using the complete occurrence data set from the area (e.g., the eastern-based model was tested in the east using 20% testing data from the east, and in the west using 100% of the occurrence data from the west) (Figure 1). Model performance was tested using Receiver Operating Characteristic (ROC) analysis (explained below); since true absence data were not available, we randomly resampled 10,000 pseudoabsence points from each area as surrogates for true absence data. ROC scores permitted an overall evaluation of model performance omitting and including each environmental variable; the most relevant environmental variables in each area were retained, and three separate environmental data subsets thus obtained.

Finally (step 2), we performed a cross-prediction analysis between western and eastern areas, searching for regional differences in invasion patterns. Using the occurrence subsets described above and the environmental data subsets selected in

Model	Training data	Testing data	Identifier
Iberian-based model	Ib_{tr} : *n*=280 (80% *Ib*)	Ib_{ts}: *n*=70 (20% *Ib*)	Ib_{tr}-Ib_{ts}
Eastern-based model	elb_{tr}: *n*=114 (80% *elb*)	elb_{ts}: *n*=28 (20% *elb*)	elb_{tr}-elb_{ts}
	elb_{tr}: *n*=114 (80% *elb*)	*wlb*: *n*=175 (100% *wlb*)	elb_{tr}-*wlb*
Western-based model	wlb_{tr}: *n*=140 (80% *wlb*)	*elb*: *n*=142 (100% *elb*)	wlb_{tr}-*elb*
	wlb_{tr}: *n*=140 (80% *wlb*)	wlb_{ts}: *n*=35 (20% *elb*)	wlb_{tr}-wlb_{ts}

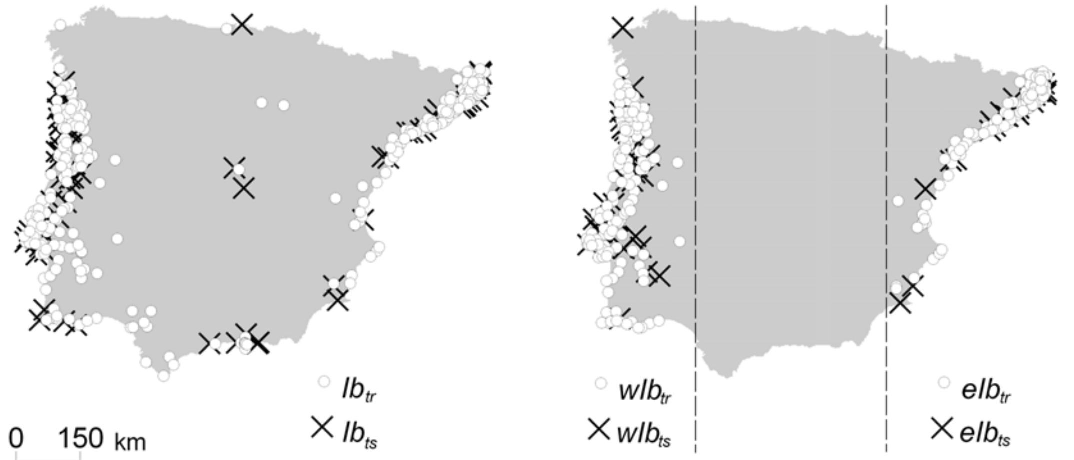


Figure 1 Description and nomenclature used for cross-prediction analyses within the Iberian Peninsula. Subsets of occurrence data from the whole Iberian Peninsula, and also eastern and western sides separately (second column), were used to develop ecological niche models, which were then projected onto the Iberian Peninsula and tested using independent occurrence data (third column). *Ib*, *elb*, and *wlb* refer to the entire occurrence sets (100% data) for the whole, eastern, and western Iberian Peninsula, respectively; Ib_{tr}, elb_{tr}, and wlb_{tr} indicate subsets of occurrences (80%) used for training the models, while Ib_{ts}, elb_{ts}, and wlb_{ts} indicate subsets (20%) used for testing model performance. The last row indicates the geographic position of each occurrences data subset for Argentine ants in the Iberian Peninsula.

step 1, we developed final models for the overall, western, and eastern Iberian Peninsula. As before, Iberian-based models were tested using independent occurrences from the whole area, whereas western and eastern-based models were each tested twice in both areas (see Figure 1). Model performance was again tested using the ROC analysis (see below).

Throughout, models were validated using the Receiver Operating Characteristic (ROC) analysis (Hanley and McNeil 1982, 1983) implemented in S-Plus (Atkinson and Mahoney 2004). ROC analysis evaluates model performance independently of arbitrary threshold for presence, and has been used extensively in distribution modeling studies owing to its nonparametric nature. Overall model performance is summarized as the area under the curve (AUC), interpretable as the probability that a model can discriminate correctly between presence and absence sites (Pearce and Ferrier 2000). AUC values range 0-1, where AUC = 1 indicates perfect model performance, and AUC = 0.5 indicates models with predictive discrimination not better than random.

Further analyses.-- Differences in model performance between modeling approaches (three levels: GARP, Maxent, GLM) and pairs of occurrence data-subset used for training and testing the models respectively (Five levels: Ib_{tr}-Ib_{ts}, eIb_{tr}-eIb_{ts}, eIb_{tr}-wIb, wIb_{tr}-eIb, wIb_{tr}-wIb_{ts}; see Figure 1) were compared using a repeated measures ANOVA using modeling approaches and pairs of occurrence data-subsets as within-subject factors.

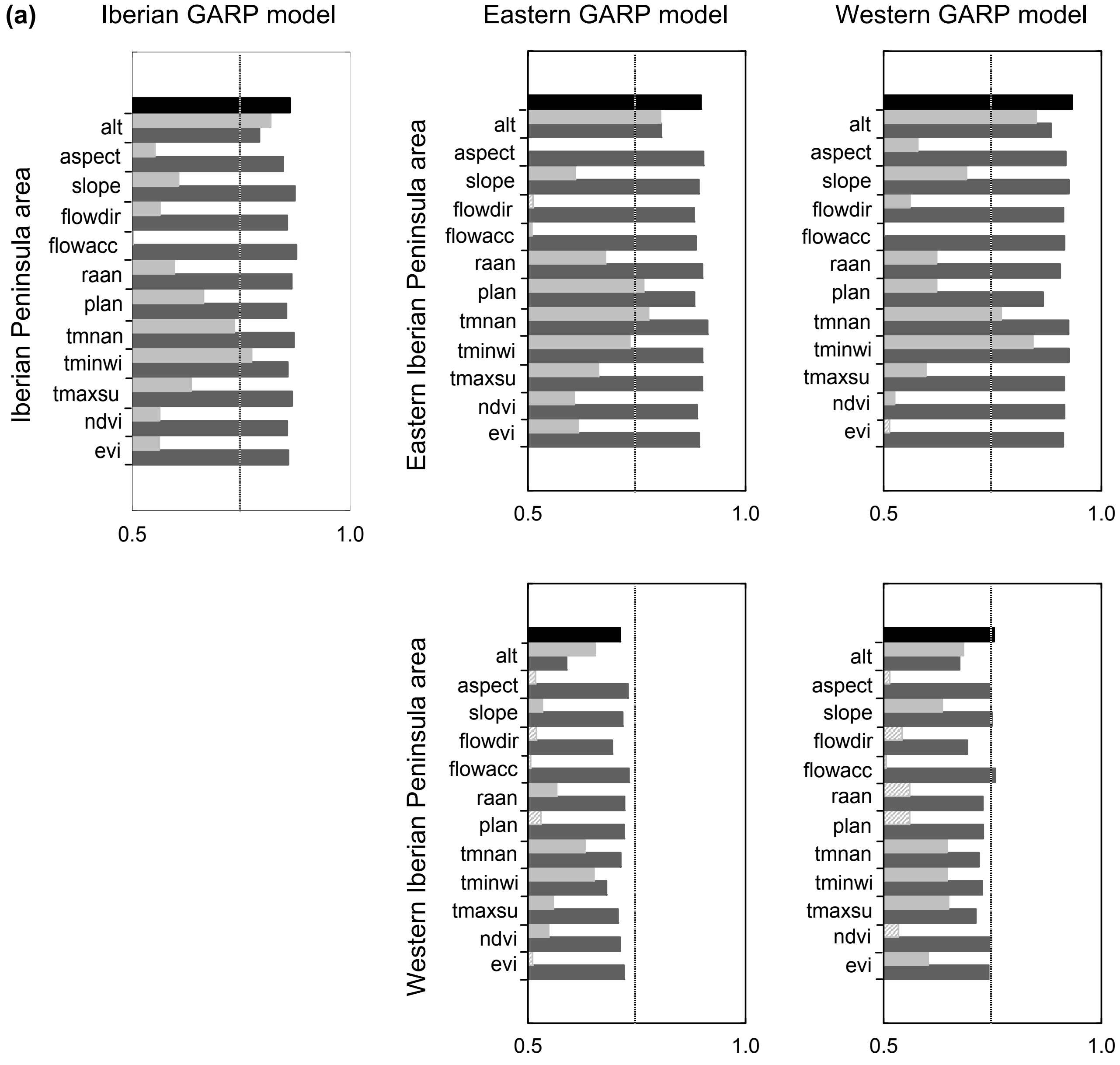
To investigate environmental relationships between eastern and western areas and occurrence localities, we performed two additional analyses. The first analysis was conducted to identify correlations among western and eastern Argentine ant occurrences. After performing a principal component analysis (PCA) using all environmental variables (topography, climate, and remotely sensed data) of eastern and western localities separately, factor coordinates of the first two principal components of each PCA were correlated to elucidate environmental similarities between the two sides of the Peninsula. The second analysis aimed to visualize (in a bivariate plot of the two main factors of a PCA) variation patterns among western and eastern areas for the most relevant variables (selected according to results of step 1) in predicting Argentine ant distribution. Given computational limitations, we randomly subsampled the overall pixels of western and eastern study areas at a 2% density for visualizations.

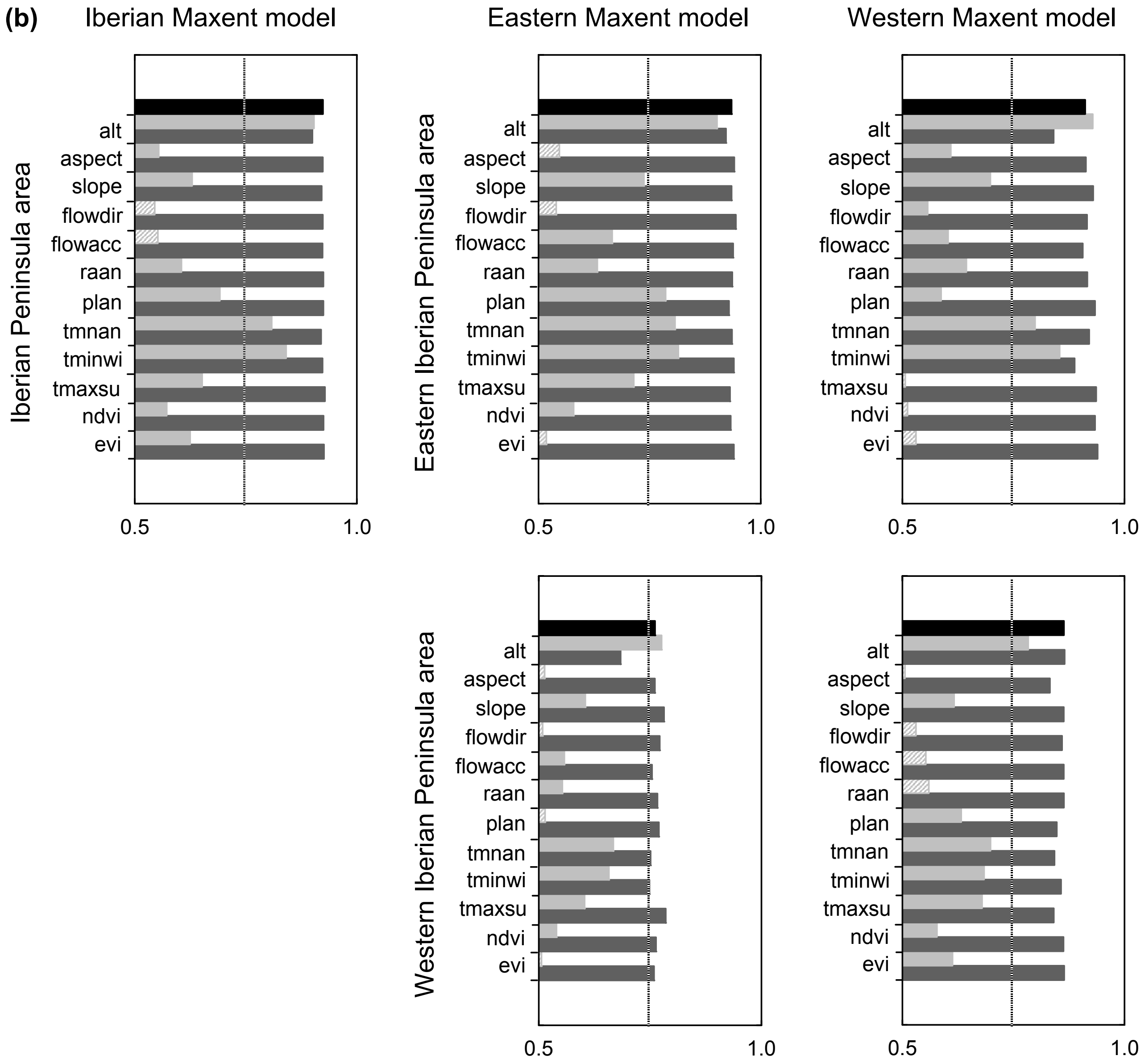
Results

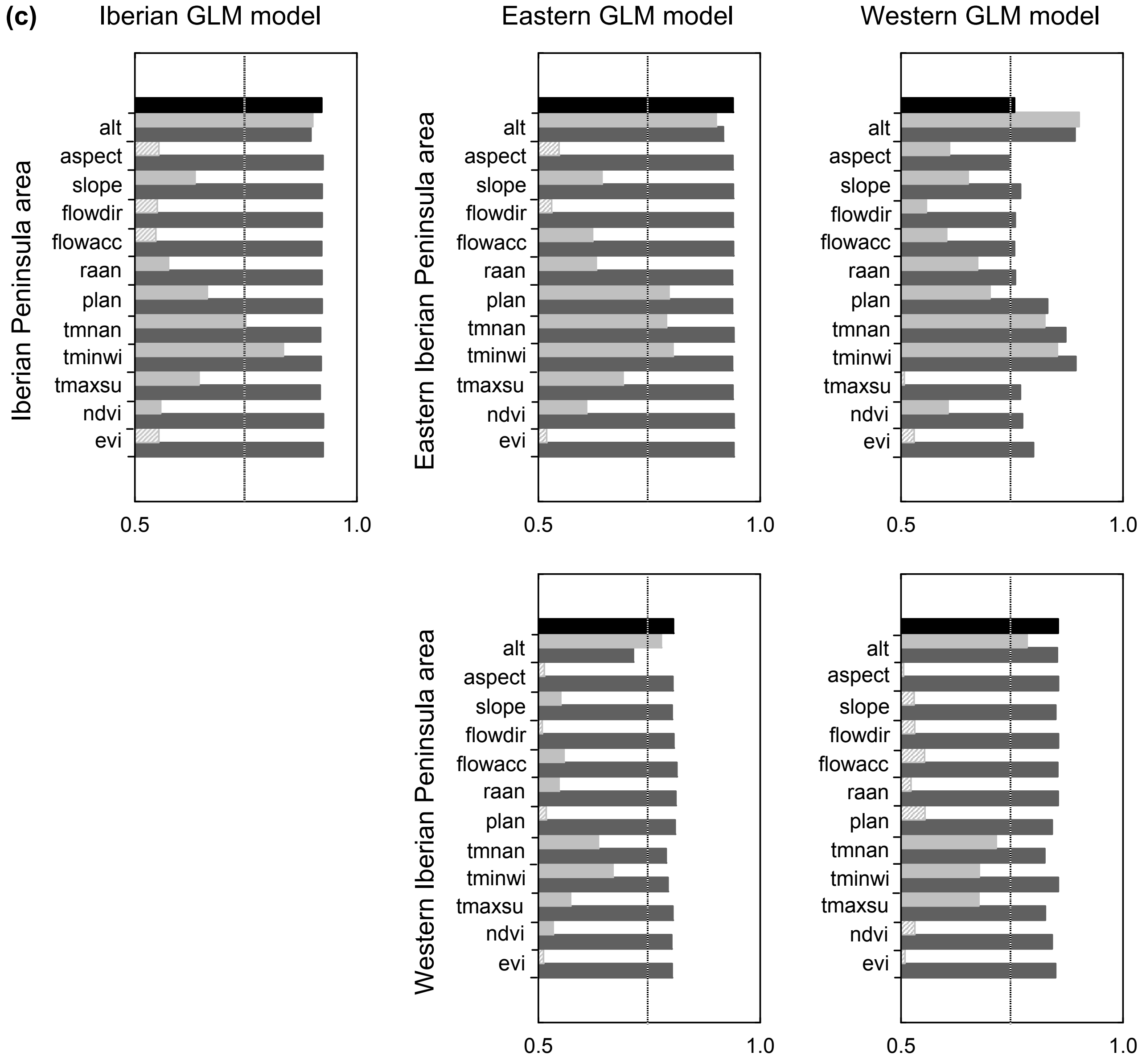
Environmental data suitability

The three modeling techniques produced similar results as to the most relevant environmental variables for predicting Argentine ant distributions in each area (Figure 2). We selected variables that contributed significantly to improvement of models, i.e. those with high AUC values when included alone in the model, and with a large AUC reduction when omitted from models generated including all other variables. For Iberian-based models, the most relevant environmental variables in predicting species distribution were *alt*, *tminwi*, and *tmnan*. Somewhat different results appeared when using eastern and western localities separately to predict both sides of the Peninsula. On the eastern area, while western-based models also indicated these three previous variables as the most suitable, eastern-based models identified *plan* as relevant as well. On the other hand, on the western area, both western and eastern-based models coincided in indicating *alt* as the only environmental variable influencing Argentine ant distribution. Finally, it is worth highlighting that western-based models gave higher AUC values in their projection to the eastern region than in the western region itself in all modeling approaches.

Figure 2 Results of the ROC analysis performed to determine the most relevant environmental variables in predicting Argentine ant distributions (step 1) using three modeling approaches: (a) GARP, (b) Maxent, and (c) GLM. For each modeling approach, columns indicate the model used for predicting Argentine ant distribution (whole, eastern, and western Iberian Peninsula-based models), whereas rows indicate the area of the independent occurrence data used to test the models (whole, eastern, and western Iberian Peninsula areas). Note that eastern and western-based models present two tests: a first test using an independent occurrence data set from the area used to build the model, and a second test with occurrence data from the area set aside from model development. Several areas under the curve (AUC) are shown for each model in each predicted area: one for the model generated using all environmental variables (black bar), twelve AUC values for models generated using only one environmental variable at a time (clearer grey bars), and finally twelve AUC for models generated leaving out one variable at a time (darker grey bars). AUC values non-significantly different from 0.5 are indicated with oblique striped bars. A dotted vertical line indicates 0.75 for visual comparison.




(b)
Iberian Maxent model
Eastern Maxent model
Western Maxent model
Iberian Peninsula area
Eastern Iberian Peninsula area
Western Iberian Peninsula area
alt
aspect
slope
flowdir
flowacc
raan
plan
tmnan
tminwi
tmaxsu
ndvi
evi
0.5
1.0


(c)
Iberian GLM model
Eastern GLM model
Western GLM model
Iberian Peninsula area
Eastern Iberian Peninsula area
Western Iberian Peninsula area
alt
aspect
slope
flowdir
flowacc
raan
plan
tmnan
tminwi
tmaxsu
ndvi
evi
0.5
1.0

According to the first additional analysis (see methods), aimed at investigating environmental correlations between eastern and western localities of Argentine ant, the principal components analyses developed on each side of the Iberian Peninsula gave similar results. The first two factors (PC1 and PC2) of each analysis were significantly correlated between both areas (r = 0.95 for PC1 and r = 0.78 for PC2). This result thus indicated that occurrence data of the species at both sides of the Iberian Peninsula are influenced in similar ways by environmental conditions. Hence, given the results reported so far, we retained 3 different environmental data sets for modeling Argentine ant distribution: (i) an optimal set for the overall Iberian Peninsula (called *ENV2*), which includes *alt*, *tminwi* and *tmnan*; (ii) a second set (*ENV1*) including *alt*, *tminwi*, *tmnan*, and *plan*, for the eastern side; and (iii) a final set (*ENV3*) for the western side, which includes *alt* alone.

Restricted to just these four environmental variables, the second analysis (see methods) intended to describe relationships between eastern and western areas and occurrence localities with the environmental characteristics of the whole Iberian Peninsula. The first two factors of the PCA accounted for 96% of total variance: PC1 (70% variance) was positively correlated with *alt* (r = 0.94), and negatively correlated with *tminwi* (r = -0.97) and *tmnan* (r = -0.97); however, PC2 (26% variation) was negatively correlated with *plan* (r = -0.98) (Figure 3). Comparisons of environmental conditions in the west versus the east indicated some differences: while the east presented a wider range of elevations (and therefore temperatures), the precipitation gradient was broader in the west. This last difference was also present in the known localities, which ranged over a broader precipitation gradient in the west.

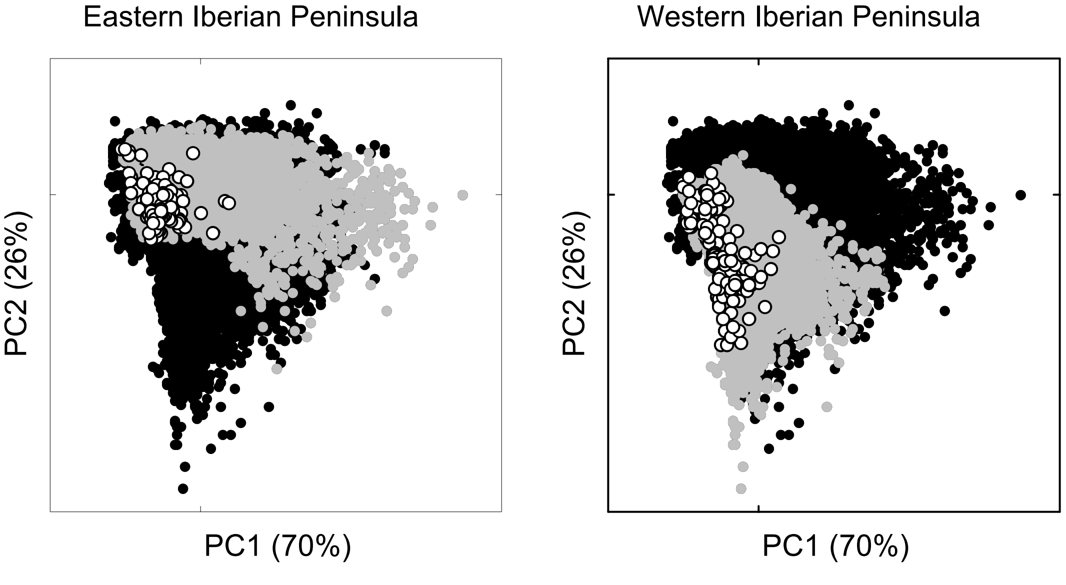


Figure 3 Visualizations of environmental conditions in the Iberian Peninsula, in a bivariate plot of two principal components, which summarize variations for the most relevant variables (*alt*, *tminwi*, *tmnan*, and *plan* according to our analysis) influencing Argentine ant distribution. Grey dots indicate the portion of environmental conditions present at the whole Iberian Penisula (black dots) covered by eastern and western areas, and white dot the portion covered by Argentine ant localities at each side.

Comparison between niche predictions.

Using the three environmental data sets (*ENV1*, *ENV2*, *ENV3*) with occurrence data set from *Ib*, *wIb*, and *eIb*, we produced final models. Model agreement between predicted distributions and known presences of Argentine ant was tested using independent occurrence data set aside from model development (Table 1), yielding AUC values of 0.62-0.94 (mean AUC = 0.83), which indicated overall good ability to predict the distribution of the species. However, variation in predictive performance between modeling approaches was statistically significant in repeated measures ANOVA ($F = 5.76$, $P < 0.001$, df = 4 for the modeling approaches factor). Highest values of model performance were attained by Maxent models (Figure 4).

Despite these differences, all modeling methodologies indicated some similar trends in Argentine ant distributions. Models developed using occurrence data from the whole Iberian Penisula give AUC values of 0.79-0.92 (mean AUC = 0.88). In cross-prediction analysis, tests performed using independent occurrence data from the same area as was used to calibrate the models gave AUC values of 0.68-0.94 (mean AUC = 0.84), whereas tests in the “other” areas gave AUC values of 0.62-0.93 (mean AUC = 0.80). Although model performance tended to be higher in areas used to calibrate models, such was not always true: for western-based models generated using Maxent and GARP, western-based models were more predictive when tested with eastern occurrences (Figure 4). This observation is corroborated by repeated measures ANOVA, which found significant differences in predictive performance between modeling approaches depending on both the calibration versus evaluation areas (F = 2.02, $P = 0.026$, df = 16 for the interaction term among factors). This result was similar to that found in step 1.

Comparisons of geographic predictions from the different models (Figure 5) also revealed some uncertainties to consider. Although, in general, all these approaches predicted similar distributional patterns, GARP predicted broader areas as suitable for Argentine ants than Maxent and GLM models. In this sense, GARP showed lower omission errors, which were balanced by higher rates of commission error, in almost all pairwise comparisons than other modeling approaches (Table 1). Considering only Iberian Peninsula-based models, despite some differences, all approaches indicated coastal areas and river valleys as highly suitable for Argentine ants. On the other hand, cross-prediction analyses indicated that eastern-based models generally predicted more restricted areas than western-based models, which in turn predicted that additional interior areas are suitable for the species.

Nevertheless, some predictions were opposite to those expected from known ecological pattern of Argentine ant when using western-based GLM models. For models developed using *ENV1* and *ENV2*, it is evident that some statistical issue does not allow correct GLM predictions of Argentine ant potential geographic distribution. Firstly, western side should have higher values of Argentine ant suitability (as shown by GARP and Maxent models); and secondly, interior areas in the northeastern part of the Iberian Peninsula should not present values as high as those predicted in the GLM analysis. Finally, special caution should be paid to predictions indicating high-elevation distributional areas (e.g., Pyrenees and Sierra Nevada mountains) as suitable for the species, such as some models based on western-based GLM models, as these predictions should prove erroneous

Table 1 Statistical results of cross-prediction analyses between eastern and western Iberian Peninsula for each modeling approach: (a) GARP, (b) Maxent, and (c) GLM, via ROC analysis. Occurrence data from the whole Iberian Peninsula (*Ib*), and also western (*wIb*) and eastern (*eIb*) sides separately, were used to develop ecological niche models (side headings of the first column delineating sections), which were then projected onto the Iberian Peninsula and tested using independent occurrence data (first column; see Figure 1 for details among cross-prediction analyses and nomenclature). Several analyses are presented for each model and testing area: general statistics as area under the curve (AUC) and its standard error (SE); omission error (percentage of occurrence data incorrectly predicted as absent) and commission index (percentage of area predicted present) at the maximized threshold; and significance in the *z* test comparing the AUCs (of the third column) among models, where A_i-A_j refers to each pair of AUCs being compared (subindices refer to the environmental data sets of the second column). All models were developed using three environmental data sets: *ENV1* (*alt*, *tminwi*, *tmnan*, and *plan*), *ENV2* (*alt*, *tminwi*, and *tmnan*), and *ENV3* (*alt*). Asterisks (*) indicates significance values of *z* tests with *P*<0.001.

(a)

model	*ENV*	AUC ± SE	threshold	omission	commission	AUC comparison
Iberian-based model						
Ib_{tr}-Ib_{ts}	1	0.84±0.018*	1	11.8	22.4	A_1-A_2: *P*<0.01
	2	0.82±0.016*	1	7.4	28.3	A_1-A_3: *P*<0.001
	3	0.79±0.015*	1	5.9	36.7	A_2-A_3: *P*<0.001
Eastern-based model						
eIb_{tr}-eIb_{ts}	1	0.89±0.029*	0.7	10.7	13.7	A_1-A_2: ns
	2	0.87±0.032*	0.2	14.3	15.8	A_1-A_3: *P*<0.001
	3	0.83±0.026*	1	7.1	27.3	A_2-A_3: *P*=0.019
eIb_{tr}-*wIb*	1	0.71±0.015*	1	27.3	37.1	A_1-A_2: ns
	2	0.71±0.019*	0.9	31.4	30.8	A_1-A_3: *P*<0.001
	3	0.67±0.012*	1	14.0	54.2	A_2-A_3: *P*<0.01
Western-based model						
wIb_{tr}-*eIb*	1	0.91±0.010*	0.8	11.4	13.9	A_1-A_2: *P*<0.001
	2	0.89±0.012*	0.9	17.9	15.6	A_1-A_3: *P*<0.001
	3	0.85±0.010*	1	7.9	24.8	A_2-A_3: *P*<0.001
wIb_{tr}-wIb_{ts}	1	0.72±0.026*	1	20.0	41.1	A_1-A_2: *P*=0.012
	2	0.69±0.030*	1	17.1	46.2	A_1-A_3: *P*=0.069
	3	0.68±0.023*	1	11.4	53.7	A_2-A_3: ns

(b)

model	*ENV*	AUC ± SE	threshold	omission	commission	AUC comparison
Iberian-based model						
Ib_{tr}-Ib_{ts}	1	0.92±0.018*	0.22	13.2	13.4	A_1-A_2: ns
	2	0.92±0.018*	0.23	13.2	13.5	A_1-A_3: *P*=0.031
	3	0.90±0.018*	0.21	17.6	17.3	A_2-A_3: *P*<0.01
Eastern-based model						
eIb_{tr}-eIb_{ts}	1	0.94±0.014*	0.03	10.7	12.4	A_1-A_2: *P*=0.080
	2	0.93±0.019*	0.05	14.3	14.4	A_1-A_3: *P*<0.001
	3	0.90±0.023*	0.09	14.3	15.7	A_2-A_3: *P*<0.001
eIb_{tr}-*wIb*	1	0.79±0.016*	0.10	25.6	25.6	A_1-A_2: ns
	2	0.78±0.017*	0.12	29.7	29.5	A_1-A_3: ns
	3	0.78±0.018*	0.11	30.8	30.8	A_2-A_3: ns
Western-based model						
wIb_{tr}-*eIb*	1	0.92±0.010*	0.18	13.6	13.6	A_1-A_2: ns
	2	0.92±0.012*	0.51	16.4	16.4	A_1-A_3: *P*=0.094
	3	0.93±0.009*	0.45	12.1	12.1	A_2-A_3: ns
wIb_{tr}-wIb_{ts}	1	0.83±0.033*	0.33	28.6	16.0	A_1-A_2: ns
	2	0.81±0.036*	0.44	25.7	19.7	A_1-A_3: ns
	3	0.78±0.038*	0.49	28.6	24.5	A_2-A_3: ns

(c)

model	*ENV*	AUC ± SE	threshold	omission	commission	AUC comparison
Iberian-based model						
	1	0.92±0.017*	0.03	14.7	14.7	A_1-A_2: ns
Ib_{tr}-Ib_{ts}	2	0.92±0.016*	0.03	14.7	14.7	A_1-A_3: $P<0.01$
	3	0.90±0.018*	0.04	17.6	17.4	A_2-A_3: $P<0.001$
Eastern-based model						
	1	0.93±0.022*	0.01	10.7	11.8	A_1-A_2: ns
elb_{tr}-elb_{ts}	2	0.93±0.023*	0.01	10.7	12.3	A_1-A_3: $P<0.001$
	3	0.90±0.023*	0.01	14.3	15.7	A_2-A_3: $P<0.001$
	1	0.81±0.014*	0.07	23.8	23.9	A_1-A_2: ns
elb_{tr}-wlb	2	0.81±0.016*	0.02	25.6	25.6	A_1-A_3: $P<0.01$
	3	0.78±0.018*	0.02	30.8	30.8	A_2-A_3: $P<0.001$
Western-based model						
	1	0.71±0.016*	0.03	30.0	30.0	A_1-A_2: $P<0.001$
wlb_{tr}-elb	2	0.62±0.014*	0.07	38.6	38.5	A_1-A_3: $P<0.001$
	3	0.90±0.010*	0.02	14.3	14.1	A_2-A_3: $P<0.001$
	1	0.81±0.036*	0.01	31.4	30.8	A_1-A_2: ns
wlb_{tr}-wlb_{ts}	2	0.80±0.038*	0.01	25.7	16.8	A_1-A_3: ns
	3	0.78±0.037*	0.02	28.6	28.6	A_2-A_3: ns

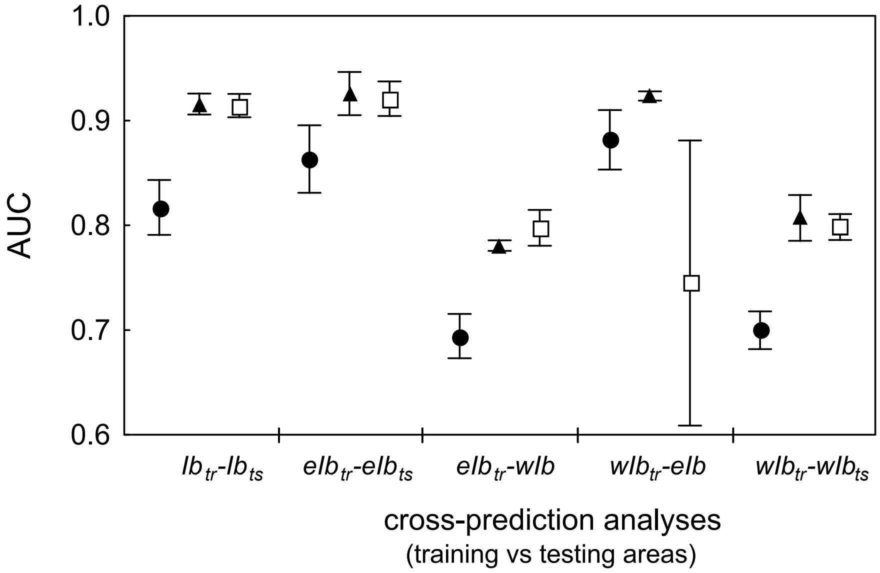
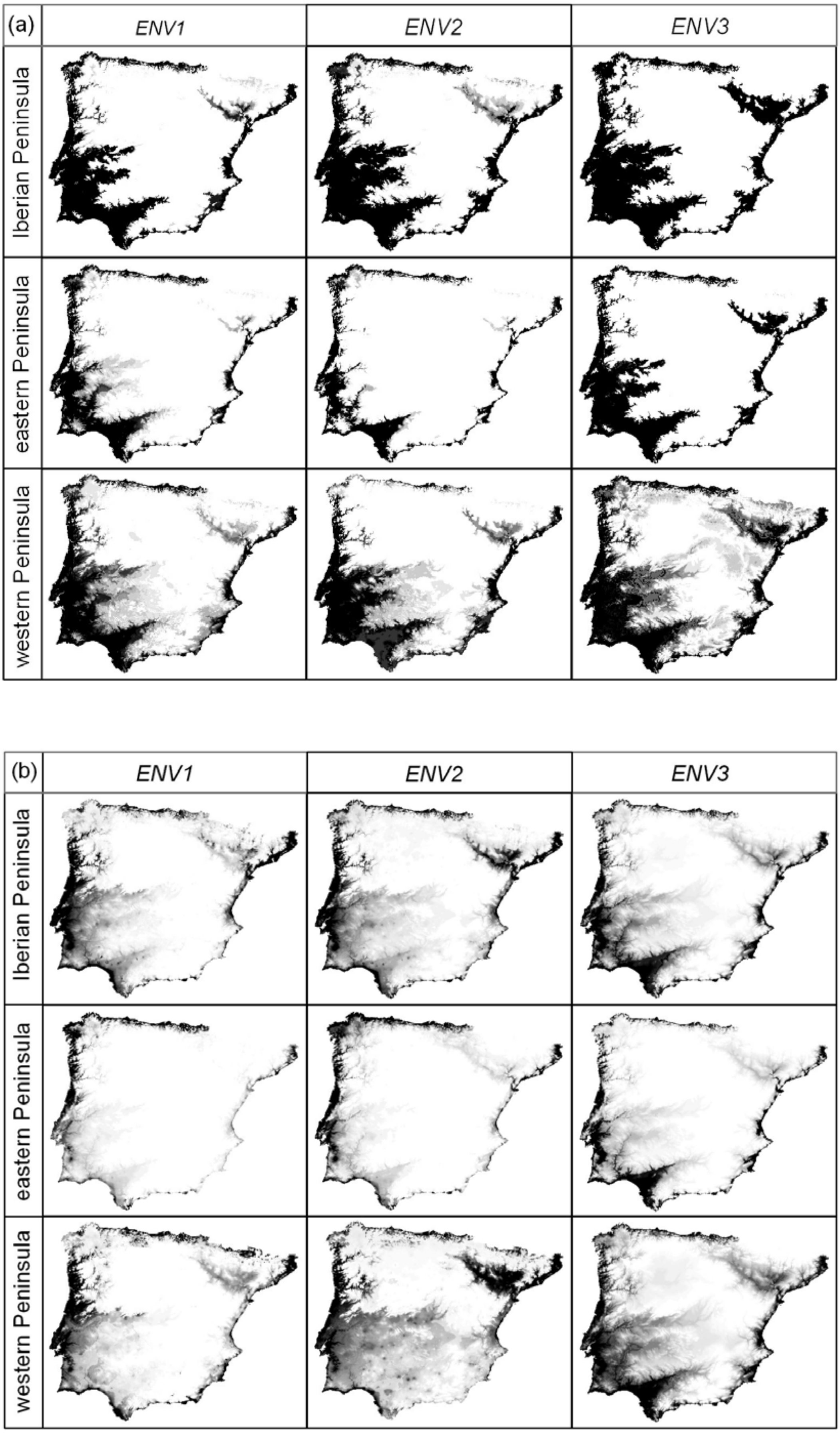


Figure 4 Differences in model performance between GARP (represented by ●), Maxent (▲), and GLM (□) modeling approaches depending on each pairs of occurrence data-subsets used for training and testing the models respectively: Ib_{tr}-Ib_{ts}, elb_{tr}-elb_{ts} and wlb_{tr}-wlb_{ts} indicate models calibrated and tested in the same area, while elb_{tr}-wlb and wlb_{tr}-elb in different areas (see Figure 1 for details on pairwise comparisons and nomenclature). *y*-axis refers to the mean AUC value of each set of predictions developed applying the same model to three environmental data set (see results section). Wiskers represent the standard error.


(a)
ENV1
ENV2
ENV3
Iberian Peninsula
eastern Peninsula
western Peninsula
(b)
ENV1
ENV2
ENV3
Iberian Peninsula
eastern Peninsula
western Peninsula

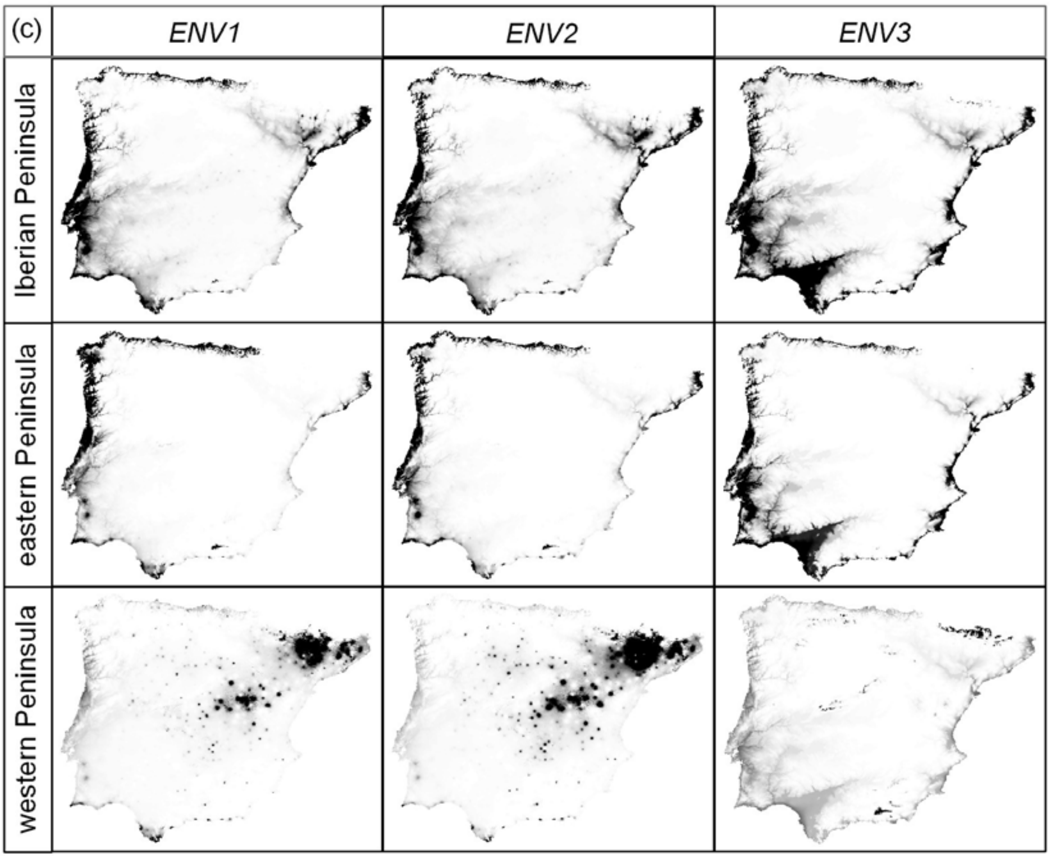


Figure 5 Predictions of the whole Iberian Peninsula, eastern, and western-based models for the Iberian Peninsula geographic area using three modeling approaches: (a) GARP, (b) Maxent, and (c) GLM. Rows indicate the occurrence data used to build the models, while columns indicate the three environmental data sets used for the predictions: *ENV1* (*alt*, *tminwi*, *tmnan*, and *plan*), *ENV2* (*alt*, *tminwi*, and *tmnan*), and *ENV3* (*alt*). Higher probabilities in predicting potential geographic distribution of the Argentine ant are indicated in darker shades.

Discussion

Comparison of modeling approaches.

We found differences among modeling approaches in both predictive performance and geographic implications. When considering only Iberian-based models (i.e., without cross-prediction analyses), the three modeling methods predicted similar areas of suitability, but GARP predicted the largest area. All three approaches gave high AUC values, and Maxent and GLM showed highest model agreement. GARP, however, showed the lowest omission in almost all pairwise comparisons. These results suggest that GARP tend to predict larger areas suitable for the Argentine ant than Maxent and GLM, which tend to fit predictions more closely to the occurrence data used to develop the models. These differences suggest that GARP is more prone to overprediction, and Maxent and GLM more prone to overfitting.

On the other hand, one should be aware of limitations of cross-prediction analyses among distributional areas (Van Horne 2002, Thuiller et al. 2004, Pearson et al. 2006). Special caution should be paid in making predictions outside the geographic range from which the model was developed, since environmental variation among regions may produce confounding predictions (Araújo et al. 2005, Elith et al. 2006). The main question is how each particular modeling technique handles the critical step of projecting a model calibrated in one area onto a new area with different conditions. GARP and Maxent successfully solve this challenge by restricting the projections to other regions to those conditions used for developing models (Phillips et al. 2006). That is, when models are extrapolated to other regions not used for calibration, areas having environmental conditions outside the calibration ranges are “clamped” (readjusted) so as not to exceed ranges of conditions present in the calibration area.

However, problems exist not only during the projection process, but also during model development. When presence data only are available to develop models, selection of pseudoabsence data is particularly important and has a significant influence on reliability of final models (Engler et al. 2004, Pearce and Boyce 2006). While Maxent and GARP selected pseudoabsence data intrinsically according to predefined and tested proportions in accordance with each method, GLM models did not presuppose use of any specific set and number of background data. Further adjustments of this aspect (such as reducing numbers of pseudoabsences included in models, or restricting pseudoabsence selection to areas not favorable for the species) may help models to fit correctly the range of environmental conditions suitable for the species. In this regard, Thuiller et al. (2004) pointed out that ecological niche models are only valid if they capture the complete response curves of environmental predictors, so extrapolating response curves of predictor variables outside the environmental calibration ranges can have (as happened with our western-based GLM models) strong implications for estimating ecological niches.

In sum, our comparisons among approaches suggest that GLM models performed less well than Maxent and GARP in predicting distributions, and that Maxent outperforms GARP as well, which coincides generally with results of other recent comparative studies (Elith et al. 2006). However, when predicting among distributional areas in the Iberian Peninsula, in essence challenging the modeling algorithms to *extrapolate* to other environmental situations, GARP outperformed Maxent in reducing omission error. GLM models failed to predict Argentine ant distributions in novel environmental situations. Between Maxent and GARP, Maxent distinguished maximally among presence and absence test data, adjusting predictions more closely to the known distributional areas of the species, whereas GARP predicted broader areas as suitable for the species and tended to capture more of its potential geographic distribution. These differences therefore lend support to the idea that Maxent is more appropriate for distribution modeling, whereas GARP is appropriate for niche modeling.

The Argentine ant in the Iberian Peninsula.

Regardless of differences in modeling approaches, accuracy of our niche models in predicting Argentine ant distributions also likely depends on occurrence sample sizes and numbers of environmental coverages included (Stockwell and Peterson 2002). Based on our previous experience with the same occurrence data set, >100 occurrence localities should be sufficient to predict Argentine ant distributions (Roura-Pascual et al. in press). On the other hand, considering environmental data, high model performance was attained with <5 variables.

Being well aware of limitations of models developed with small numbers of environmental data sets (Peterson and Cohoon 1999), we included the *ENV1* dataset to provide a view of the influence of elevation as a predictor variable in our analysis. In general, all models developed seemed highly dependent on elevation. In addition to elevation, however, climatic variables (mean minimum winter temperature, mean annual temperature, mean annual precipitation) were important in refining predictions of Argentine ant potential distributions (Figure 2). This result is consistent with knowledge of the species, which is not known to occur in coldest areas at highest elevations of the Iberian Peninsula (Espadaler and Gómez 2003), and also with the spatial resolution of our analyses, which does not allow us to consider smaller-scale processes that can restrict the species' distribution locally, such as anthropogenic disturbance or presence of watercourses (Menke and Holway 2006).

Overall, our results (Table 1, Figure 5) indicated that Argentine ants on both sides of the Iberian Peninsula have similar ecological niches. While results of the first additional analysis (see results) indicated that Argentine ant occurrences on both sides are correlated similarly and with the same environmental variables, high AUC values in cross-prediction analyses between areas corroborated that similarities were not random, but rather were owing to similar ecological conditions during invasion. Small differences between western and eastern predictions suggest that populations on the western side of the Iberian Peninsula may occupy a slightly wider range of environmental characteristics than those of the eastern side. Hence, western-based models projected to the eastern areas overpredict distributions, which could explain why western models tested on the eastern side show higher AUC values than the same models tested in the west.

Visual comparisons of known Argentine ant localities and predicted distributions, given current ranges, suggest that further expansion of the species is still possible along the coast and inland along river valleys. Since river courses make it easy for the species to enter far inland into the Iberian Peninsula, preventive efforts should be made along the Ebro, Guadalquivir, Guadiana and Tajo rivers to avoid future expansions into these areas. Moreover, the northern and southeastern coasts appear extremely suitable for the Argentine ant, so further research is necessary to determine the species' real distribution in those areas.

The differences between western and eastern Iberian Peninsula invasions by Argentine ants could result from two causes: (i) earlier arrival on the western coast than on the eastern one, allowing the species to expand farther there than on the eastern side; or (ii) existence of small differences in the species' ecological niche between western and eastern populations of the Iberian Peninsula. Real ecological niche differences between western and eastern populations, not due to modeling artifacts (Roura-Pascual et al. in press), could results from different origins of introduced populations as the existence of two supercolonies of Argentine ant seems to indicate (Giraud et al. 2002). However, since the first cited reference of Argentine ant occurrence in the Iberian Peninsula appeared on the western side (1894 in Oporto), earlier than on the eastern side (1923 in Valencia, probably 1919; (Espadaler and Gómez 2003), we cannot conclude with certainty that these slight divergences are due to real ecological niche differences.

Conclusions

Further research on the utility of cross-prediction in the ecological niche modeling processes is still needed (Thuiller et al. 2004, Araújo et al. 2005, Guisan and Thuiller 2005, Elith et al. 2006, Pearson et al. 2006), since this type of modeling analysis offers valuable insights into mechanisms in invasion or extinction processes (Wiens 1989, Wiens and Graham 2005, Fitzpatrick et al. in press). Instead of avoiding projections of the species distribution outside the spatial or temporal range used to calibrate the models, new improvements to reduce uncertainties in such practices should be explored (Araújo et al. 2005, Peterson 2005, Pearson et al. 2006).

As a next step in understanding Argentine ant invasions in the Iberian Peninsula, broad systematic sampling inventory is necessary to determine the details of the species' distribution in the region (Hirzel and Guisan 2002). Availability of a reliable presence/absence data set would definitely permit improvements in model performance, and improved models would help managers to establish more effective measures to prevent further expansions. Moreover, further local-scale studies should be carried out to identify fine-scale ecological factors affecting the spread of the species at different spatial scales (Van Horne 2002, Farina et al. 2005).

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Chapter 5

Local-scale risk assessment of an invasive species (*Linepithema humile*) via ecological niche models

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Abstract

Determining the geographical extent and ecological suitability range of an invasive species is a challenge for most ecologists concerned about management practices. In the absence of detailed data on the real distribution of species, ecological niche models offer the opportunity to estimate the potential range limits of an invasion and also to better understand the ecological processes acting at different spatial scales. Herein, generalized additive models (GAM) are used to determine the distribution of the Argentine ant (*Linepithema humile*), a highly widespread invasive species native to South America. Occurrence data mostly obtained from two different sampling strategies were combined with environmental data at different resolutions in order to predict the geographical extent of the ant invasion in Catalonia across spatial scales. Comparisons between models suggest that the species is still expanding in the northeastern area of the Iberian Peninsula, especially along the Costa Brava where the Argentine ant is not in equilibrium with its environment. In general, models at regional and local scales indicate that coastal areas are highly suitable for the species. However, more detailed field work studies (especially at the invasive front) are needed to determine the dimensions of the invasion in inland areas.

Introduction

An important consequence of globalization is the increase in biotic exchange among regions worldwide (Vitousek et al. 1997, Sala et al. 2000). The movement of species far away from their native ranges produces a gradual replacement of native biota (Mack et al. 2000), often exacerbating the ecological and societal impacts of changes on biodiversity (Chapin et al. 2000, Olden et al. 2004). Under these circumstances, several authors (Lodge and Shrader-Frechette 2003, Perrings et al. 2005) claimed for the urgent need to establish large-scale and long-term management strategies to prevent and/or reduce the dispersal and establishment of non-native species. A key requirement for implementing an effective strategy is the identification of those areas potentially suitable for the species (Hulme 2003). As such, modelling practices predicting potential distributions of non-indigenous species are acquiring of great importance among ecologists assessing invasion limits (Peterson 2003, Thuiller et al. 2005).

Among the world’s worst invasive species (http://www.issg.org/database/) are several widespread ant species which are severely threatening the world’s ant biodiversity (McGlynn 1999, Holway et al. 2002a). One of these highly invasive ants is the Argentine ant (*Linepithema humile*), a species native to South America, now established in many Mediterranean and subtropical areas worldwide (Suarez et al. 2001). In the Iberian Peninsula, the Argentine ant is mainly distributed along the Atlantic and Mediterranean coasts, although it has also been observed in some inland areas. In Catalonia (NE Iberian Peninsula), the species is known to be patchily distributed along coastal areas (Espadaler and Gómez 2003).

The distributional pattern of the Argentine ant is explained by two different types of dispersion: diffusion spread through budding, and long distance jump dispersal associated to humans (Suarez et al. 2001). In a forested area of the Gavarres-Cadiretes massif (NE Catalonia), Casellas (2004) reported that the Argentine ant spread by budding at a mean rate of spread of 19.00±6.83m per year (n = 1). Even though assuming a constant net yearly expansion of the invasion throughout the area, dispersion by budding will not be sufficient for the Argentine ant to attain its present-day distribution at the northeastern side of the Iberian Peninsula. Contrarily, after the first human-mediated jump-dispersal events responsible for the introduction of the species in the Iberian Peninsula, subsequent jump dispersions through human commerce and transportation to other areas far away from the sites of introduction almost certainly explain most its present distribution. The first reported observations of the Argentine ant in the Iberian Peninsula date back to 1894 in Oporto (western side) and 1923 -probably 1919- in Valencia (eastern side) (Espadaler and Gómez 2003), but in the absence of a detailed study on the invasion history we cannot conclude that the current distribution of the species has been originated only from these two foci. Quite the opposite: the importance of harbours in NE Iberian Peninsula on the transatlantic commercial routes (Barbaza 1988, Yáñez 1996) leave the way open to consider that the Argentine ant could have been introduced directly from its native range into the northeastern area of the Iberian Peninsula, and possibly into other coastal areas. However, the strong relationship between Oporto (Portugal) and cork industries in NE Iberian Peninsula (Barbaza 1988) could also have been the cause of long-distance dispersions of Argentine ant populations within the Peninsula. In any case, once established into a new area, the Argentine ant spreads locally through a diffusion-like process into neighbouring urban or natural areas (Suarez et al. 2001, Carpintero et al. 2004, Holway and Suarez 2006).

Previous studies have determined the influence of environmental factors in shaping Argentine ant distribution at different scales (Way et al. 1997, Human et al. 1998, Holway et al. 2002b, Krushelnycky et al. 2005, DiGirolamo and Fox 2006, Menke and Holway 2006). Most of them recognize the crucial influence of climatic data (particularly temperature and humidity) in determining the species distribution, as well as the importance of vegetation (both by changing soil moisture, and increasing resource availability) and anthropogenic disturbances. On the other hand, biotic resistance from native ants (since in the case of the other invasive species currently known in the Peninsula, *Lasius neglectus*, there is little competition with *Linepithema humile* (Espadaler and Collingwood 2000, Reyes and Espadaler 2005)) only seems to limit the expansion of Argentine ant in those areas presenting unsuitable and stressful environmental conditions.

As such, because of the ecological and economic impacts caused by the Argentine ant invasion (Vega and Rust 2001, Holway et al. 2002a) and also because of the urgent need to establish preventive measures to avoid further expansions of the species, the major aim of this study is to determine the potential distribution of the Argentine ant in the northeastern area of the Iberian Peninsula. Due to the influence of the spatial scale in ecological processes (Wiens 1989), we predicted the Argentine ant distribution at regional (Catalonia) and local (Costa Brava, northeastern Catalonia) scales to elucidate possible divergences in the invasion depending on the scale of analysis. Occurrence (derived from specimen collections and mostly field work sampling) and environmental data influencing species distribution at different scales are thus combined into a statistical model to assess the role of environmental factors, and predict those areas most suitable for the species. Despite being aware of the limitations of such modelling practices when applied to invasive species not in equilibrium with its environment (mainly due to the inclusion of present-day absence data in localities that meet all requirements for the species, but are not yet invaded due to the history of the invasion process) (Hulme 2003, Menke and Holway 2006), predictions of Argentine ant potential distribution indicate those areas that should be vigilant in preventing future introductions, and also provide a better understanding of the invasion at finer spatial scales. Divergences in the invasion process are investigated along a north-south gradient along the coast, as well as between coastal and interior areas, searching for historical and ecological differences in the Argentine ant distribution at the northeastern side of the Iberian Peninsula.

Methods

The approach used to predict Argentine ant geographic distribution is based on modelling its ecological niche (Peterson 2003, Guisan and Thuiller 2005), which appears to be a long-term stable environmental constraint (Peterson et al. 1999). Niche models are constructed by relating occurrences of the species (in the form of latitude/longitude coordinates) with combinations of environmental data (in the form of GIS coverages) influencing its distribution. These are then projected onto geographic dimensions to identify those areas most appropriate for the species (Soberón and Peterson 2005).

We used Generalized Additive Models (GAM) to predict Argentine ant distribution at fine scales on the basis of presence/absence occurrence data, and to elucidate the most influential environmental variables. The use of GAM in ecological studies with predictive purposes is not new, and they have been widely applied and validated in several studies (Guisan et al. 2002, Thuiller 2003, Elith et al. 2006). GAM are semi-parametric generalizations of usual linear regression models, which allow for non-parametric and complex relationships between the response and predictor variables in addition to the parametric forms (Hastie and Tibshirani 1990, Guisan et al. 2002). A non-parametric smoothed function of all the explanatory variables is fitted to the response variable without prejudging the shape of the relationship between both terms. As a consequence it attains more complex response curves than most classical lineal models. We used a cubic spline smoother, and the appropriate level of smoothness for each predictor was automatically fitted during the stepwise selection methodology. We applied an automatic forward stepwise procedure using Akaike's information criterion (AIC (Akaike 1974)) to select the most parsimonious models in S-Plus software.

Model validation was assessed using the area under the curve (AUC) index of the Receiver Operating Characteristic (ROC) analysis (Hanley and McNeil 1982, 1983) implemented in S-Plus, using the Atkinson and Mahoney (2004) ROC functions. ROC analysis evaluates the ability of a model to discriminate correctly between presences and absences of the species independently of an arbitrary threshold at which presence might be accepted. The AUC corresponds to the ROC curve derived from plotting *sensitivity* (presence data correctly predicted as present) versus *1-specificity* (absence data incorrectly predicted present) at different thresholds simultaneously. Good model performance is characterized by large areas maximizing *sensitivity* for low values of *1-specificity*, and *z* values above the critical level: AUC range from 0 to 1, where values of 0.5 indicate model discrimination no better than random and values of 1 highest model agreement. Comparisons between two areas under the curve for different models were also performed.

Modelling approach at regional scale (Catalonia)

Occurrence and environmental datasets.-- Occurrence data was composed of 77 absences and 125 presence localities extracted from specimens in personal collections (Espadaler and Gómez 2003), and a field survey on urban areas carried out during the summer of 2003 (Figure 2). The main human settlements in Catalonia were surveyed during half an hour searching for Argentine ant occurrence data (both presence/absence). Although different sites were surveyed within each urban area, only the most central geographic coordinate (in the form of longitude/latitude) was recorded to characterize the position of the species' occurrence data. See Annexe 3 and 4 for a complete list of the occurrence data.

Environmental data included 12 digital coverages summarizing aspects of topography [mean elevation (herein abbreviated as *alt*), northern aspect (*aspect*)[17], slope (*slope*), and topographic position index (*tpi*), derived from the Digital Elevation Model of Catalonia, native resolution 30 x 30 m; ICC[18]], climate [annual solar radiation (*raan*), annual mean precipitation (*plan*), annual mean temperatures (*tmnan*), minimum winter mean temperatures (*tminwi*), and maximum summer mean temperatures (*tmaxsu*)[19], from the Climatic Digital Atlas of Catalonia[20], native resolution 180 x 180 m; (Ninyerola et al. 2000)], remotely sensed data [16-day composites for the Normalized Difference Vegetation Index (*ndvi*) and for the Enhanced Vegetation Index (*evi*) from July 2005 from the NASA-MODIS/Terra data set[21], native resolution 250 x 250 m (Justice et al. 1998)], and distances to several environmental features [seacoast (*dsea*), water courses (in a logarithmic scale, *lgdriv*), and urban areas (in a logarithmic scale, *lgdurb*), derived from vectorial coverages of the Ministry of Environmental and Housing of the Government of Catalonia[22]. The environmental data was selected according to present-day knowledge of the species: the influence of temperature and humidity in determining its distribution, and also on annual cycles of species activity (Holway et al. 2002b, Abril 2005, Krushelnycky et al. 2005, DiGirolamo and Fox 2006, Heller et al. 2006, Menke and Holway 2006). The topographic position index was calculated in relation to neighbouring areas at 1000m distance using a GIS extension that classifies the landscape into landform categories (Jenness 2005), which indirectly influence Argentine ant presence (Holway 1998). All data were prepared and resampled at 180 m spatial resolution in ArcView 3.2 and ArcGIS 8.2 for the analysis.

Modelling approach.-- For modelling Argentine ant potential distribution at regional scale (Catalonia), we restricted our analysis to urban areas (distance <180m from urban areas appearing on the Land Uses Map of Catalonia, native resolution 2 x 2m; CREAF[23]), since extrapolations to non-urbanized areas could be erroneous taking into account the nature of the sampling method. As indicated previously, we first performed a forward stepwise procedure using all occurrence data to select the most relevant predictor variables. Secondly, we used this reduced environmental data set with a randomly selected subset of occurrence data (75%) to calibrate the predictive models, which were then projected back onto the landscape to determine Argentine ant potential distribution in Catalonia. Models were validated on the remaining 25% occurrences using ROC analysis.

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[17] Aspect was transformed to a continuous variable by measuring the percentage of 30 x 30 m pixels with values of 250-360º and 0-70º within each 180 x 180 m pixel. This transformation was required for developing GLM, which do not handle categorical data, and summarizes northward-facing tendency of slopes.

[18] http://www.icc.es/

[19] Mean winter minimum temperatures were obtained by calculating the mean of December, January, February and March minimum temperatures; and maximum summer mean temperatures by calculating the mean of May, June, July, August, September, and October maximum temperatures. Months were selected according to known details of Argentine ant activity; the period from May to October is when the species is mosy active, exceeding the summer season according to Abril (2005).

[20] http://magno.uab.es/atles-climatic/

[21] http://edcimswww.cr.usgs.gov/pub/imswelcome/

[22] http://mediambient.gencat.net/cat/el_departament/cartografia/inici.jsp

[23] http://www.creaf.uab.es/mcsc/

Modelling approaches at local scale (Costa Brava)

Occurrence and environmental data sets.-- Occurrence data for the Costa Brava consists of 1302 absences and 1027 presences data points (in the form of longitude/latitude coordinates) extracted from a field survey carried out during the summers of 2004 and 2005 (Figure 2). The main roads of the Costa Brava were surveyed at intervals of 500-1000m distance, searching for Argentine ant presence/absence data within a radius of 10m from the stopping site over 10 minutes. The geographic coordinates of the site were recorded with a GPS to characterize the occurrence data of the species. However, these initial 2330 occurrence localities were reduced to 1937 (1120 absences and 817 presences) to avoid an excessive density of occurrences, which would overfit the models, in some areas subjected to intensive sampling. In these areas, we randomly selected around 5 occurrence localities per 2x2km^2 extension. See Annexe 5 for a complete list of the occurrence data. This dataset at local scales do not include occurrences from the Catalonia dataset at regional scales, since localities from both datasets are not comparable because were obtained at different resolutions using different sampling methods.

Similarly to the regional scale approach, the environmental dataset included 13 coverages summarizing aspects of topography (mean altitude, mean slope, topographic position index, derived from the Digital Elevation Model of Catalonia, native resolution 30 x 30 m; ICC[18]), climate (annual solar radiation, annual precipitation, annual mean temperatures, mean winter minimum temperatures, and mean summer maximum temperatures[19], from the Climatic Digital Atlas of Catalonia[20], native resolution 180 x 180 m; (Ninyerola et al. 2005)), remote sensing data (one monthly composite for the Normalized Difference Vegetation Index (NDVI) and for the Enhanced Vegetation Index (EVI) of July 2005 from the NASA-MODIS/Terra data set[21], native resolution 250x250m; (Justice et al. 1998)), and other distance-related coverages (distance to the seacoast[24], and main water courses, and urban areas). The selection of these environmental variables followed the previously mentioned criteria. Distance to water courses (derived from the rivers' vector coverage of the Ministry of Environmental and Housing of the Government of Catalonia[22]) and urban areas (derived from the Land Cover Map of Catalonia, native resolution 2x2m, CREAF[23]) (Holway et al. 2002b, Carpintero et al. 2004) were log-transformed before the analyses. All data were prepared and resampled at 30 m spatial resolution in ArcView 3.2 and ArcGIS 8.2 for the analyses.

Modelling approach.-- As previously done for the regional model, we restricted our Costa Brava analysis to roads (distance <60m from the roads' digital coverage of the Ministry of Environmental and Housing of the Government of Catalonia[22]) and urbanized areas (distance <30m from urbanized areas appearing on the Land Uses Map of Catalonia, native resolution 2 x 2m; CREAF[23]). At this local scale, three main questions arise: (1) is the Argentine ant invasion in equilibrium with its environment on the Costa Brava, or are further expansions to be expected in the future?, (2) is the Argentine ant invasion pattern identical all along the coastal areas of the Costa Brava?, and (3) does the Argentine ant occupy different ecological niches in coastal and inland areas of the Costa Brava?

In order to test the first question (*Question 1*), the previous model predicting Argentine ant distribution at regional scales (Catalonia) is compared with a similar model built at local scales (Costa Brava) using different environmental and occurrence data sets. Since the regional model is based on a wider range of ecological

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[24] Distance to the sea was only considered as a predictor variable for modeling the Argentine ant distribution throughout the overall Costa Brava, but not for comparisons along the coastal gradient and between coastal and inland areas. In the latter cases, the variable was already implicitly included into the model by subsetting the occurrence data.

characteristics than the local model, predictions at regional scales are thus expected to reflect the ecological potential of the Argentine ant on the Costa Brava more closely than the local model. As such, if the prediction at local scales is very far removed from regional predictions, the Argentine ant is still expected to undergo further expansions at local scales.

To develop the model at local scales, as before, we performed a forward stepwise procedure using the overall occurrences dataset to select the most relevant environmental variables for determining species distribution throughout the Costa Brava. Final models were then calibrated using 75% of the original occurrences (in combination with the final predictor variables), and the remaining 25% to validate the predictions using ROC analysis.

To elucidate possible differences in the Argentine ant invasion pattern along the latitudinal, and also ecological, gradient of the Costa Brava (*Question 2*), we restricted our analysis to the areas comprised between the coastline and 4 km inland. Three areas were differentiated according to main water basins and the main topographic and geologic units: Cap de Creus (herein called CC), Golf de Roses-Massís de Begur (RB), and Gavarres-Cadiretes massifs (GC) from North to South. The Cap de Creus is a schistous massif strongly influenced by northern winds (characterized by their high speed), with mediterranean shrubland vegetation. The Golf de Roses-Massís de Begur presents an heterogeneous landscape mainly composed of sedimentary, intensively cultivated plains and small calcareous and siliceous massifs (mainly covered by kermes oak forests accompanied by aleppo pines), considerably shaped by human presence. The Gavarres-Cadiretes massif is a low granite mountain range mainly covered by cork oak forests, highly influenced by nearby urban concentrations. All three areas are affected by fast-growing urbanization processes, which are strong in the North and near the coastline.

We performed the forward stepwise and the calibration of final models using all localities available in each area, to take advantage of each occurrence data subset. In total, four models were developed: one model using all coastal occurrences (ALL) (363 absences and 588 presences), and three models using subsets of these coastal occurrences for each area (56 absences and 20 presences for CC, 153 absences and 122 presences for RB, 154 absences and 446 presences for GC). Model validation was tested within each area using a checkboard test, and between areas applying a cross-validation process using ROC analysis. Because model performance depends critically on the occurrence data used for calibrating the model (Fielding and Bell 1997), the checkerboard approach forces the model to predict into areas from which no occurrences were used to built the model (Peterson and Shaw 2003). Each specific subset of localities was classified into two categories (*t1* and *t2*) depending on their location on a 5 x 5 km checkerboard grid. Ecological niche models based on localities in one category were used to predict the distribution of the other occurrence category and vice versa, and the respective area under the ROC analysis curve calculated using the independent occurrence data aside from model calibration. The number of occurrences per area and per category were: *t1*=572 and *t2*=379 for ALL, *t1*=40 and *t2*=36 for CC, *t1*=132 and *t2*=143 for RB, and *t1*=400 and *t2*=200 for GC areas.

Finally, searching for possible ecological differences between coastal and inland invasion patterns (*Question 3*), we restricted our analysis to the Gavarres-Cadiretes massif and the surrounding 4 km. The whole Gavarres-Cadiretes is a siliceous massif extending from sea level to an altitude of 535m, extensively covered by cork oak forests, traditionally exploited by cork industries. Following the water basins, the massif naturally separates the study area into coastal and inland areas. The coastal side of the massif is characterized by sandy beaches and rocky cliffs with a temperate climate due to the influence of marine fog, while inland areas have more extreme climatic conditions with winter atmospheric inversions. The massif is surrounded by large urban concentrations (mainly the coastal area), which grew considerably in the late 60-70s.

Herein, we also performed the forward stepwise and the calibration of the final models using three different subsets of occurrence data: one subset with the occurrences available for the whole massif (composed of 614 absences and 565 presences), and two subsets for coastal (246 absences and 497 presences) and inland (368 absences and 68 presences) areas. Model performance was also validated using a checkboard test within each area, and a cross-validation process between areas using ROC analysis. The number of occurrences per occurrence data set and per category was: *t1*=660 and *t2*=519 for the whole, *t1*=456 and *t2*=287 for coastal, and *t1*=204 and *t2*=232 for inland areas.

Results

Predicted distribution at regional scale (Catalonia)

The urban survey in Catalonia corroborates the invasive pattern described by Espadaler and Gómez (2003), which restricts Argentine ant distribution near the coast and suggests that the species is absent from inland and high altitude urban areas (Figure 2). Northern occurrences were more or less the same as those indicated by previous authors, but new localities invaded by the Argentine ant were found in southern Catalonia. However, in general, the Argentine ant occupies more interior areas in northern than in southern areas, where the species is present at lower distances from the sea.

Stepwise procedure determined six environmental variables as necessary for modelling Argentine ant distribution in Catalonia, where *dsea* and *alt* have the greatest influence (Figure 1). Models built using this reduced set of environmental data present high model performance (AUC=0.94±0.03, $P<0.001$), and suggest urban areas along the coast (the most remote at 60 km distance) as highly suitable for the Argentine ant (Figure 2).

Predicted distribution at local scale (Costa Brava)

On the other hand, the road survey at local scales indicates that the almost continuous species distribution in the Costa Brava described by the previous urban survey is further fragmented into several invasion processes presenting different degrees of spatial continuity. The southernmost coastal area (near the Gavarres-Cadiretes massif) is where the species attains its maximum occurrence (Figure 2). Northern areas show a more disperse invasion pattern, and some sites are occupied by the Argentine ant while totally absent from the surroundings. Similarly, the Argentine ant is almost absent from inland areas and it is only present in some isolated localities near urban settlements.

Eight environmental variables were selected during the stepwise process as influencing Argentine ant distribution in the Costa Brava, the most relevant being *dsea*, *tmnan*, *plan* and *lgdurb* (Figure 1). The test assessing the accuracy of the Costa Brava model developed using this subset of predictor variables indicates good model agreement in predicting species occurrence (AUC=0.82±0.02, $P<0.001$). Predictions indicate that a further spread of the species is still possible near the coast and in southernmost interior areas (Figure 2). These results are somewhat different from those obtained by the regional model, which predict almost all urban areas of the Costa Brava as highly suitable for the Argentine ant.

Comparing predicted distributions along a coastal gradient

Focusing our attention on the coastal area, Argentine ant occurrence varies from one region to another (Figure 4). Species presence increases towards the southernmost coastal areas of the Costa Brava. GC presents a more widespread and continuous mosaic of invaded localities than RB and CC areas, where the species has a patchy distribution. In the CC area, although the species is mainly present near human dwellings, it was also found invading natural environments. The Argentine ant was known to invade natural habitats in the GC and RB areas (J. Bas personal observation), but this pattern was not known to occur until now in northern areas (CC) with more extreme environmental conditions.

Stepwise procedures were applied to the whole coastal area and in each specific area selected between 6-7 environmental variables. *plan*, *tmaxsu* and *lgdurb* were retained in all cases (Figure 3). Considering each area separately, the most influential predictor variables are: *plan*, *tmnan* and *lgdurb* in the whole coastal area; *alt*, *tminwi* and *lgdurb* in GC; *tmaxsu* and *lgdurb* in RB; and *evi* and *lgdriv* in CC. It is also important to notice the influence of *lgdriv* on CC and RB areas.

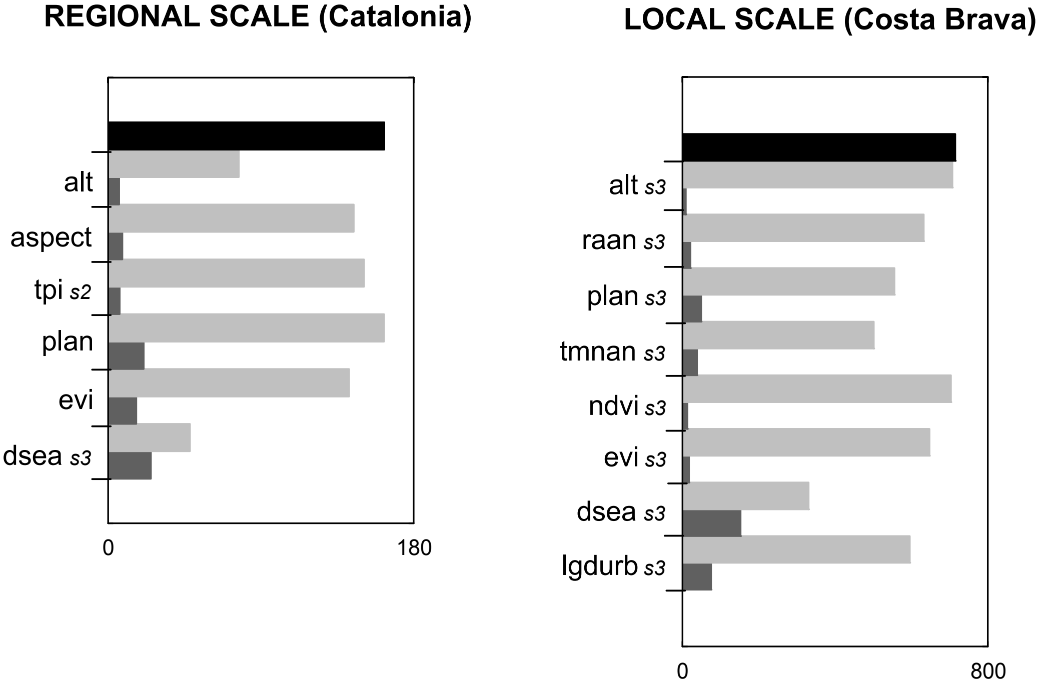

Figure 1 Relative contribution of each predictor variable included in the Argentine ant models at regional and local scales. *s2* and *s3* indicate the degree of smoothness. Environmental variables not included in the final full models are not shown. Lighter grey bars are proportional to the difference in deviance between the final full model and a model with only that variable alone, and darker grey bars proportional to the difference in deviance between the final full model and a model with that variable excluded. Black bars indicate the difference in deviance between the final full model and the null one. Deviance values of both regional and local full models are 106.68 and 1922.80 respectively. (See methods section for an explanation of abbreviations).

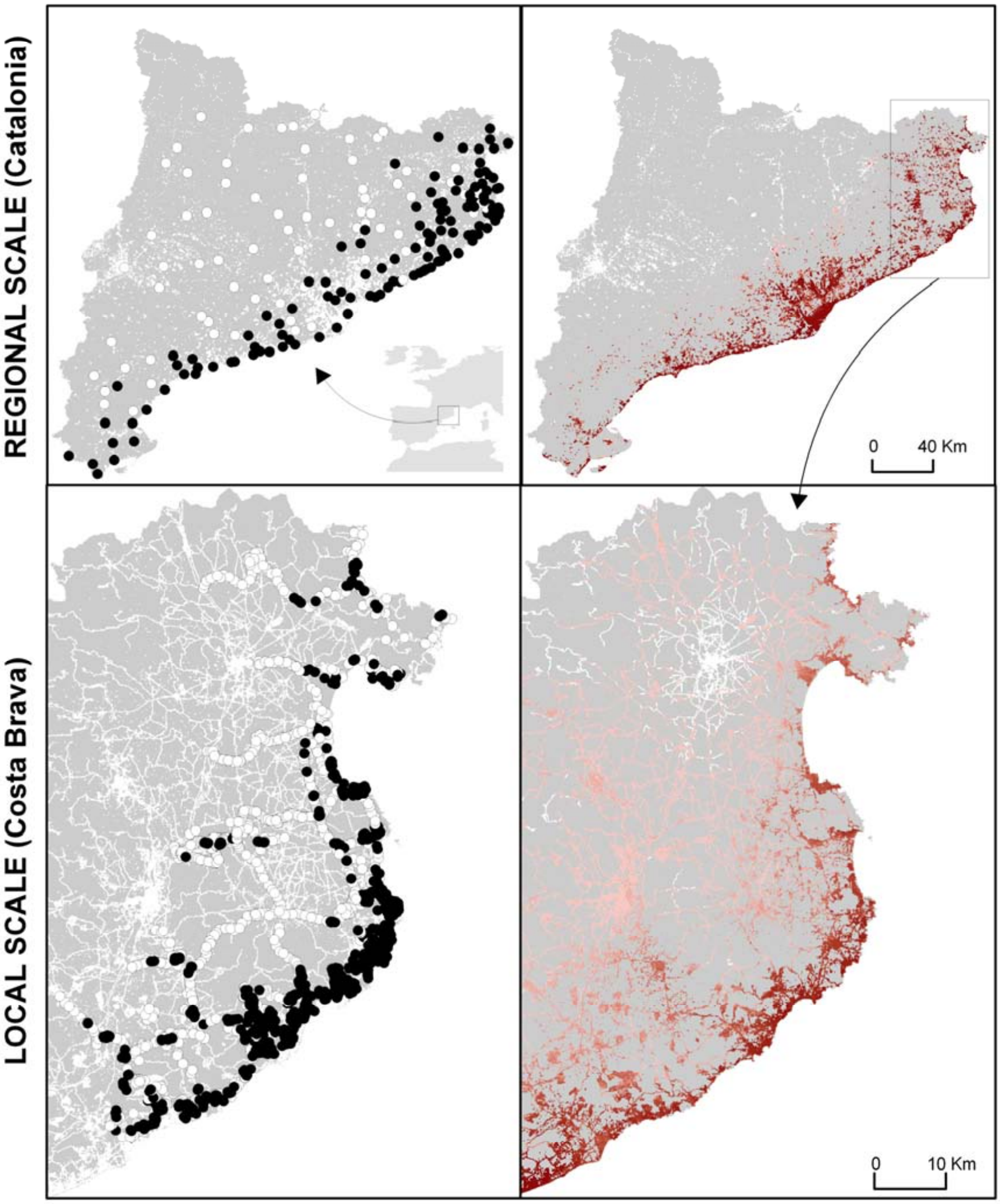

Figure 2 Predicted potential distribution for the Argentine ant at different spatial scales. Rows indicate both regional and local models, while columns show the occurrence data used to calibrate the models (absences in white dots, and presence in black dots) and the final projections respectively. Darker red shades indicate higher probabilities in predicting potential geographic distribution of the Argentine ant.

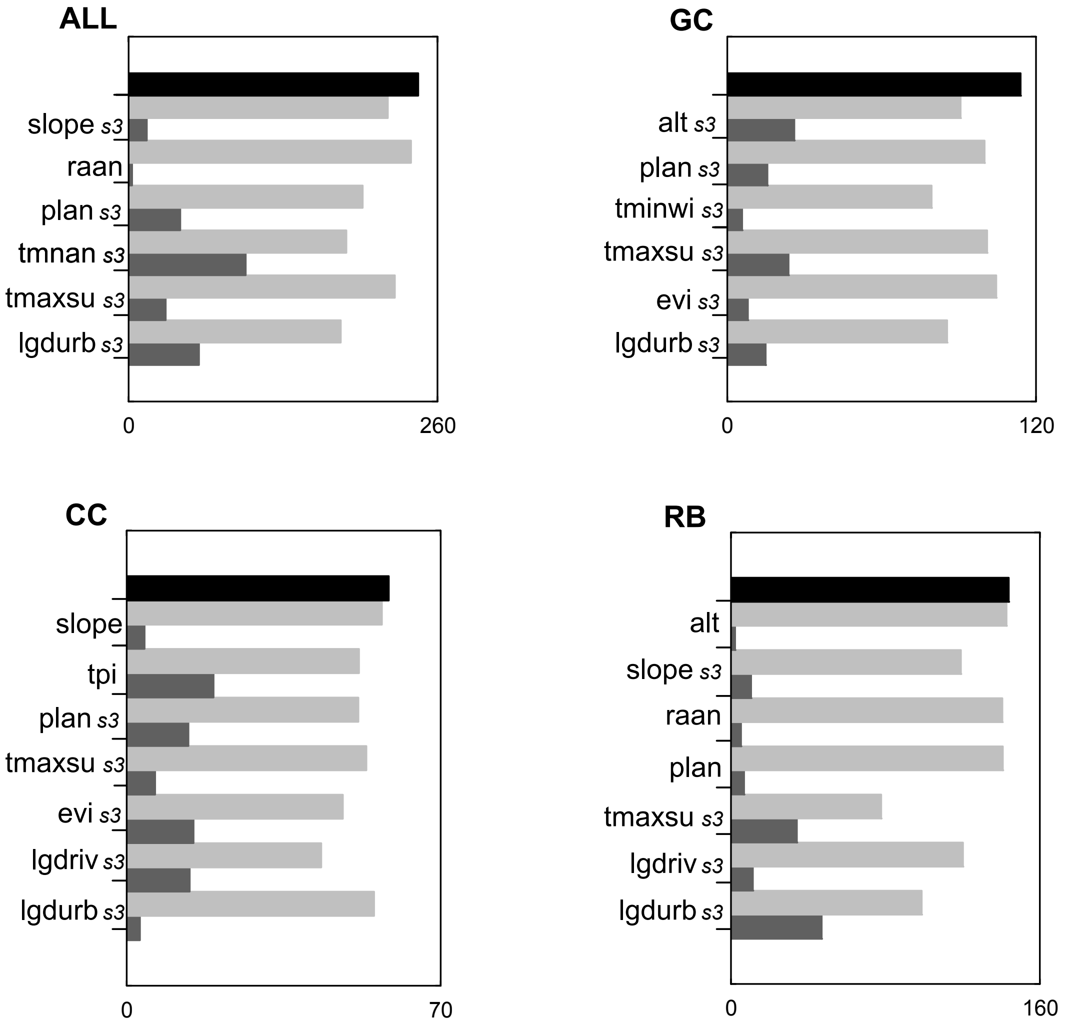

Figure 3 Relative contribution of each predictor variable included into the Argentine ant models developed along the Costa Brava using four different occurrence datasets (ALL, CC, RB, and CC). *s2* and *s3* indicate the degree of smoothness. Predictor variables not included in the final full models are not shown. Lighter grey bars are proportional to the difference in deviance between the final full model and a model with only that variable alone, and darker grey bars proportional to the difference in deviance between the final full model and a model with that variable excluded. Black bars indicate the difference in deviance between the final full model and the null one. Deviance values for each developed full model are: 1020.69 for ALL, 29.11 for CC, 233.76 for RB, and 569.45 for GC. (See methods section for an explanation of abbreviations)

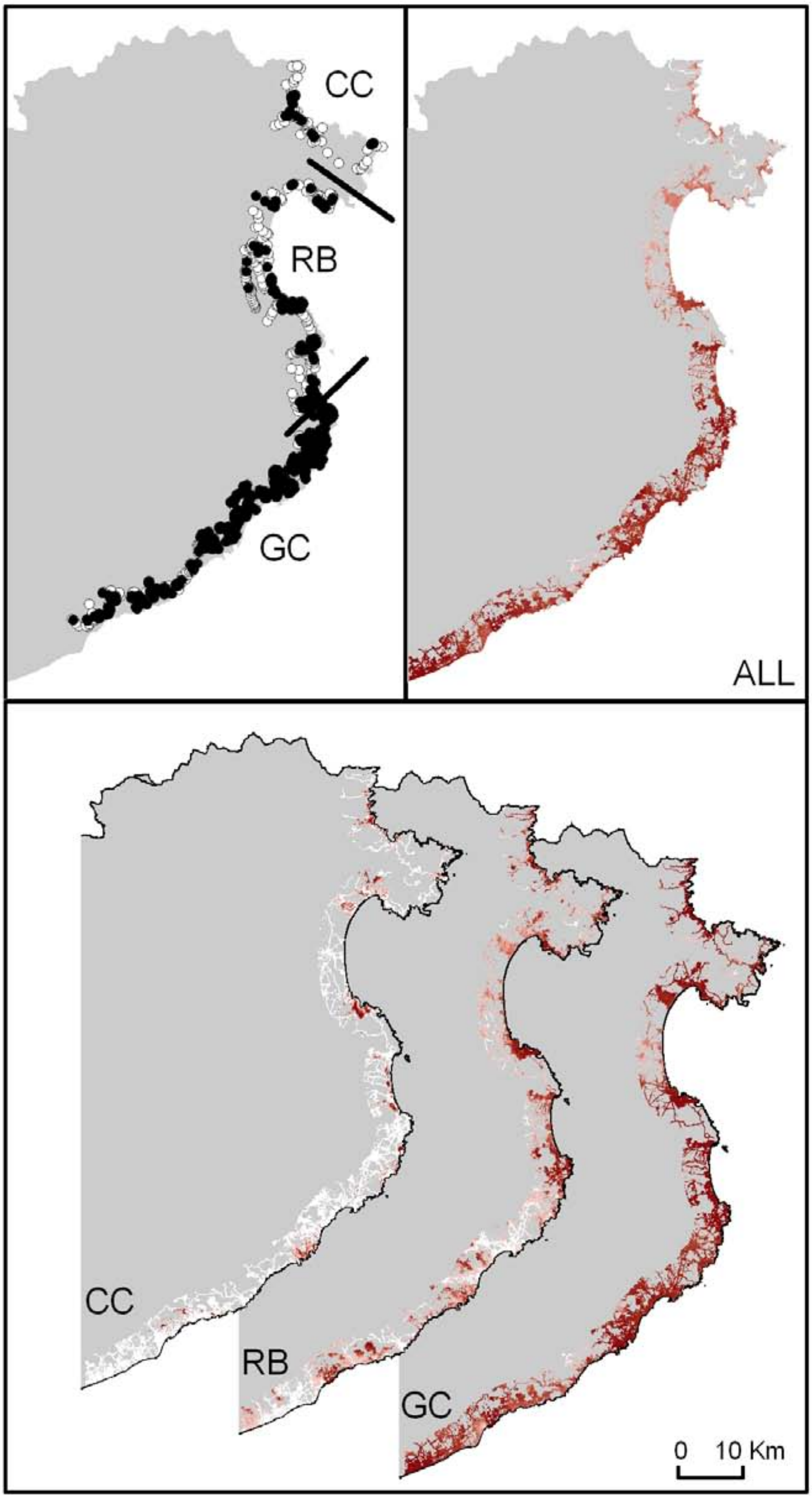

Figure 4 Predicted potential distribution for the Argentine ant along the Costa Brava using four different occurrence data sets to calibrate the models: one dataset using overall localities at less than 4km from the sea (ALL), and three subsets of this previous set as indicated in the upper-left figure (CC, RB, and CC). Darker red shades indicate higher probabilities in predicting potential geographic distribution of the Argentine ant. (See methods section for an explanation of abbreviations).

Table 1 Model performance of Argentine ant predicted distribution along the coastal band of the Costa Brava using different calibration occurrence data sets (ALL, CC, RB, and GC). The statistic presented is the area under the curve of ROC analysis (herein represented by A with a subindex, indicating the occurrence data used to calibrate the model), its standard error and the significance of the *z* test. The first row indicates tests performed within the same area using a checkboard test, while the second row shows tests between areas. The third row shows only those pairwise comparisons among the AUCs of the second column that are non-significant, or with low significance values of *z* test. Tests were measured using independent occurrence data, except those cases highlighted in italics. Asterisks indicate the significance of *z*-tests: * for *P*=0.05-0.01, and ** for *P*<0.01. (See material and methods section for an explanation of abbreviations)

	ALL	CC	RB	GC
Test within areas	A_{t1}: 0.72±0.02**	A_{t1}: 0.87±0.06**	A_{t1}: 0.80±0.04**	A_{t1}: 0.66±0.03**
	A_{t2}: 0.77±0.02**	A_{t2}: 0.83±0.07**	A_{t2}: 0.74±0.04**	A_{t2}: 0.72±0.04**
Test between areas	_A_{ALL}: 0.77±0.02**_	_A_{ALL}: 0.67±0.08*_	_A_{ALL}: 0.77±0.03**_	_A_{ALL}: 0.69±0.03**_
	_A_{CC}: 0.56±0.02**_	_A_{CC}: 0.98±0.01**_	A_{CC}: 0.68±0.03**	A_{CC}: 0.59±0.03**
	_A_{RB}: 0.52±0.02_	A_{RB}: 0.56±0.07	_A_{RB}: 0.88±0.02**_	A_{RB}: 0.56±0.03*
	_A_{GC}: 0.61±0.02**_	A_{GC}: 0.57±0.07	A_{GC}: 0.70±0.03**	_A_{GC}: 0.77±0.02**_
AUC comparisons	A_{CC}-A_{RB}	A_{ALL}-A_{GC}	A_{ALL} -A_{CC}*	A_{CC}-A_{RB}
	A_{CC}-A_{GC}*	A_{ALL} -A_{RB}	A_{CC}-A_{GC}	
		A_{RB}-A_{GC}		

Model validation within each area using the checkboard test gives AUC values ranging from 0.66 to 0.87 (mean AUC 0.76), where the GC model has the lowest values and CC, the highest ones (Table 1). However, in general, results suggest good model performance in predicting Argentine ant distribution in each area. Visualizations of the GC-based models (Figure 4) indicate the whole coastal band of the Costa Brava as highly suitable for the Argentine ant, to some extent overpredicting the current species distribution in RB and CC areas. On the other hand, RB and especially CC-based models tend to predict smaller extensions suitable for the Argentine ant and leave out localities where the species is known to occur. Tests between all three areas using independent occurrence data (that is using the occurrence data of each area set aside from model development) give AUC values ranging from 0.56 to 0.70, where those predictions to RB show the highest values of model performance (Table 1).

Comparing predicted distributions of coastal and interior areas

In concordance with previous results, the coastal band of the Gavarres-Cadiretes massif has the highest density of the Argentine ant (Figure 6). Not only restricted to urban areas, the species has already invaded considerable extensions of natural habitats and is still spreading into further areas (Casellas 2004). In inland areas of the massif, the Argentine ant has a patchy distribution near human settlements, even though it has also been found occupying natural habitats quite a distance away from human dwellings. This latest finding is extremely important because it shows the species' ability to invade interior natural habitats, which was not known to occur until now in the northeastern part of the Iberian Peninsula.

From 3 to 9 predictor variables were selected during the stepwise procedure (Figure 5), and *raan* and *lgdurb* were the only environmental variables kept at all the areas (whole, coastal and inland areas of the massif). Those most influential variables in each area are *plan*, *tminwi* and *tmaxsu* for the whole massif; *alt*, *tminwi*, *tmaxsu* and *lgdurb* for coastal areas; and *tpi*, *raan* and *lgdurb* for inland areas.

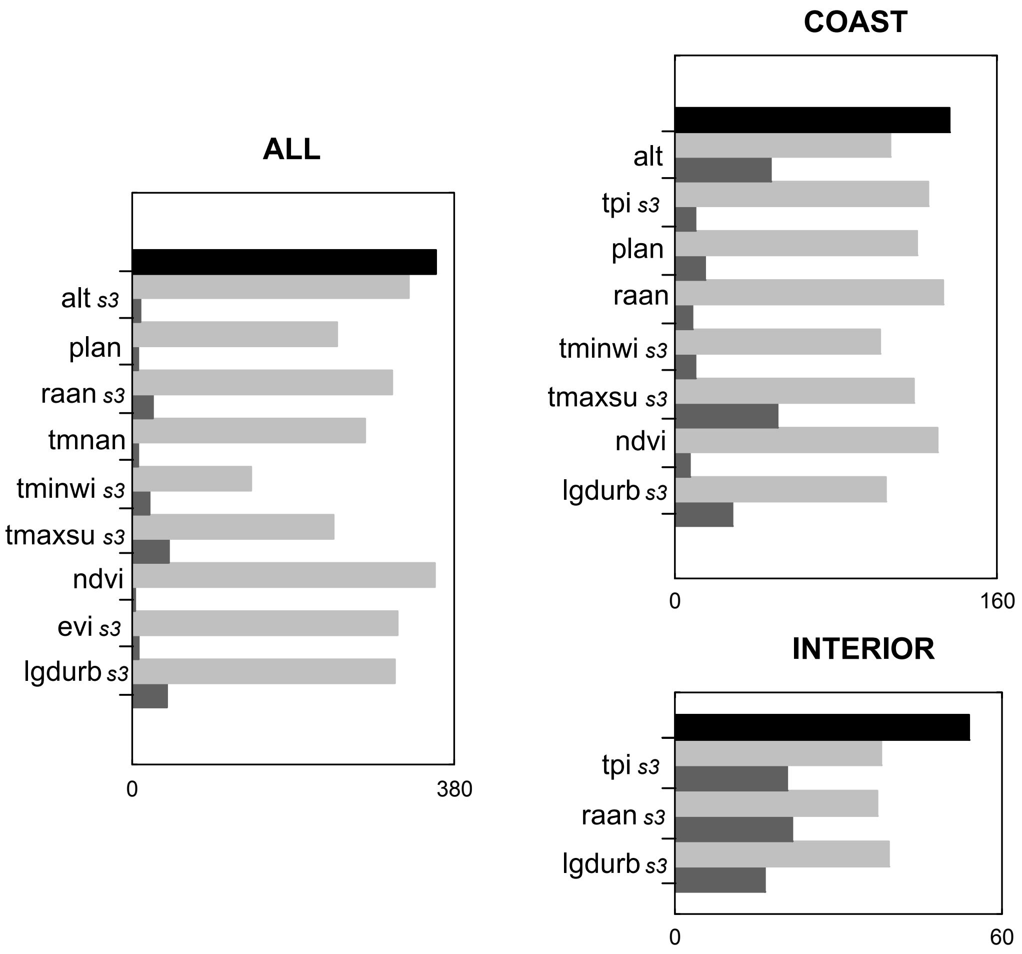

Figure 5 Relative contribution of each predictor variable included in the Argentine ant models developed on the Gavarres-Cadiretes massif using three different occurrence datasets: overall occurrences (ALL), only occurrences on the coastal (COAST) and interior (INTERIOR) areas separately. *s2* and *s3* indicate the degree of smoothness Predictor variables not included in the final full models are not shown. Lighter grey bars are proportional to the difference in deviance between the final full model and a model with only that variable alone, and darker grey bars proportional to the difference in deviance between the final full model and a model with that variable excluded. Black bars indicate the difference in deviance between the final full model and the null one. Deviance values for each developed full model are: 1273.74 for ALL, 806.98 for COAST, and 323.49 for INTERIOR.

Tests performed within each area give AUC values ranging from 0.66 to 0.76 (Table 2), indicating the usefulness of these models to predict Argentine ant distribution. However, there are some differences between predictions (Figure 6). The overall-based model suggests coastal areas as the most appropriate for the species, while high altitude and inland areas are predicted as un- or less suitable. Contrarily, although coast-based models predict higher suitability values than interior-based models, both models indicate inland and high altitudinal areas as also appropiate for the species. However, cross-validation tests between areas give values of model performance that are not significantly different from random predictions (Table 2), indicating that models calibrated in one area do not predict the Argentine ant distributions in the other area correctly.

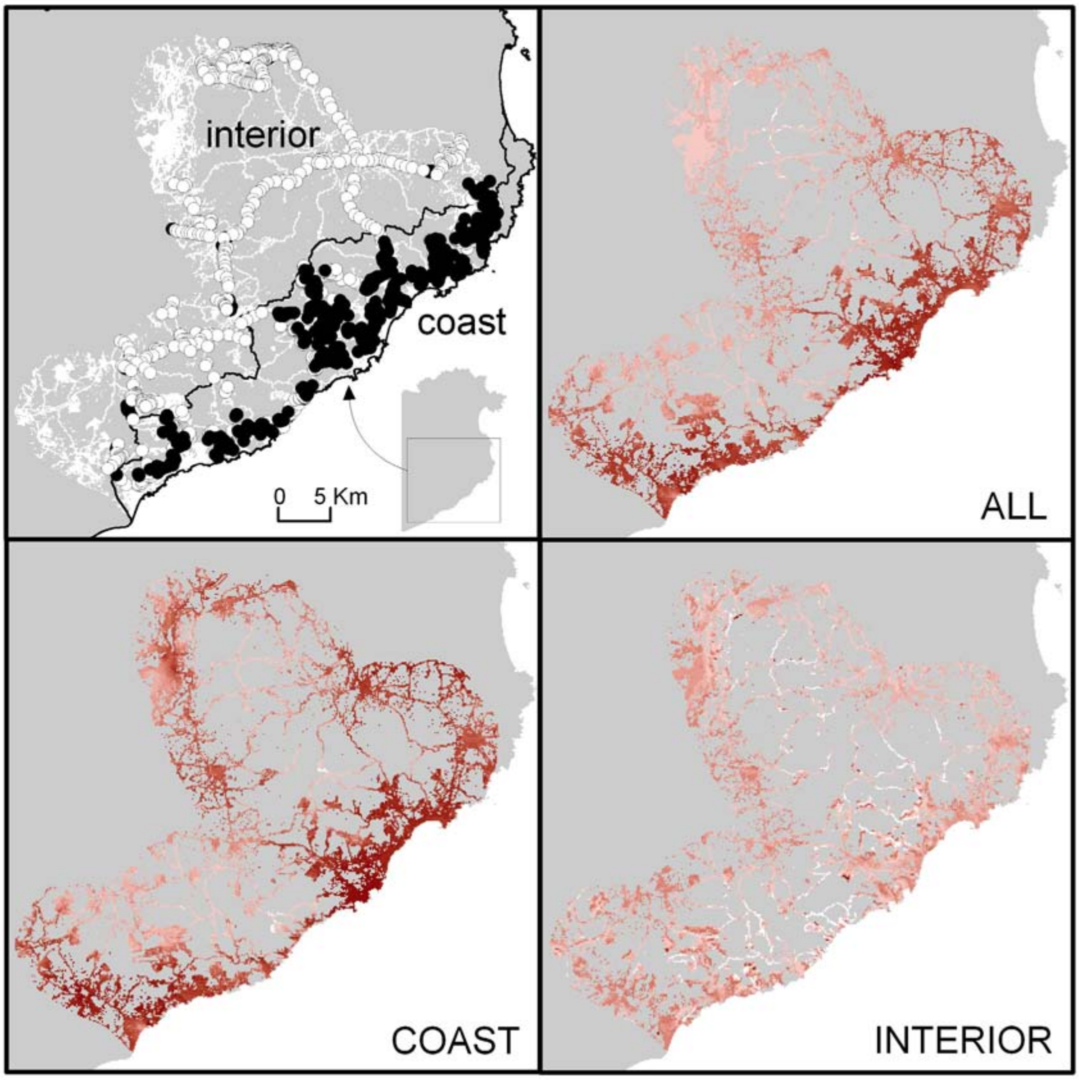

Figure 6 Predicted potential distribution for the Argentine ant on the Gavarres-Cadiretes massif using three different occurrence data sets to calibrate the models: one data set using overall occurrences (ALL), and two subsets of this previous set for coastal (COAST) and inland (INTERIOR) localities separately, as indicated on the upper-left figure. Darker red shades indicate higher probabilities in predicting potential geographic distribution of the Argentine ant.

Table 2 Model performance of Argentine ant predicted distribution on the Gavarres-Cadiretes massif using three different calibration occurrence data sets: overall occurrences (ALL), only occurrences on the coastal (COAST) and inland (INTERIOR) areas separately. The statistic presented is the area under the curve of the ROC analysis (herein represented by A with a subindex, indicating the occurrence data used to calibrate the model), its standard error and the significance of the test. The first row indicates tests performed within the same area using a checkboard test, while the second row shows tests between areas. The third row shows only those pairwise comparisons among the AUCs of the second column that are non-significant, or with low significance values of z test. Tests were measured using independent occurrence data, except those cases highlighted in italics. Asterisks indicate the significance of *z* tests: * for *P*=0.05-0.01, and ** for *P*<0.01.

	ALL	COAST	INTERIOR
Test within areas	A_{t1}: 0.74±0.02** A_{t2}: 0.76±0.02**	A_{t1}: 0.66±0.03** A_{t2}: 0.70±0.03**	A_{t1}: 0.67±0.06** A_{t2}: 0.68±0.04**
Test between areas	*A_{ALL}:0.80±0.01*** *A_{COS}:0.76±0.01*** *A_{INT}: 0.53±0.02*	*A_{ALL}:0.71±0.02*** *A_{COS}:0.75±0.02*** A_{INT}: 0.52±0.02	*A_{ALL}:0.59±0.03*** A_{COS}:0.53±0.04 *A_{INT}: 0.78±0.03***
AUC comparisons			A_{ALL}-A_{COS}

Discussion

Question 1: Is the Argentine ant invasion in equilibrium with its environment?

Urban and road surveys at regional and local scales attempt to characterize the Argentine ant invasion in the NE Iberian Peninsula, and update and complement the previous work of (Espadaler and Gómez 2003). Both surveys describe the distribution of the species in Catalonia and the Costa Brava, respectively, and at the same time reveal the existence of geographic differences among species occurrence within each area. These differences could be due to artefacts of the sampling procedure (different sampling intensity in different areas) or real differences in the species' geographic distribution among regions. At the same time these real differences could be due to temporal (the invasion is at a less advanced stage, and therefore more non-true absence data included in the database) or ecological reasons (geographic barriers to invasion or ecological niche differences). Since biases on the occurrence data were reduced by standardizing the sampling strategies, geographic differences in the occurrence data seem likely to be due to ecological reasons. Indeed, observations of the invasion during the field survey at local scales indicate that the Argentine ant is still invading new environments and it thus highlights that the species is probably not in equilibrium with its environment.

Under these circumstances, modelling invasive species distribution is an extremely difficult task when the species is not in equilibrium. Occurrence data do not reflect the entire ecological potential of the invasion, so niche models developed with this limited dataset are somewhat misleading with regards to the true invasive potential of the species. As such, while areas predicted as highly suitable for the species are prone to invasion, non-suitable areas cannot be considered as such. In this way, although the niche model at regional scale predicts the Argentine ant near the coast, expansions of the invasion into further interior and high altitudinal areas with low temperatures should also be taken into greater consideration to determine the exact geographic dimensions of the invasion in Catalonia (Espadaler and Gómez 2003).

In the area of the Costa Brava, the niche model at local scale generally predicts less suitable areas for the Argentine ant than the model at regional scale. Although the model at local scales correctly predicts the occurrence data of the road survey, it omits some urban localities where the species is known to occur. Given that the model at regional scales has been built based on a wider range of environmental conditions (since occurrences also occupy a wide spectrum of ecological conditions) than the model at local scales, it tends to capture a larger proportion of the potential geographic distribution of the Argentine ant in the Costa Brava than the local model itself. The local model, in counterpart, adjusts predictions more close to the know distributional areas of the Argentine ant in the area. Predictions at local scale are thus misleading in relation to the potential distribution of the species in the Costa Brava area, due to the inclusion of non-real absences in the model. In this sense, Bolliger et al. ((2000) in Thuiller et al. (2003)) state that regional models are more robust than local models in predicting species distribution, even in those cases where the species is not in equilibrium. Thus, differences between regional and local predictions also indicate that the Argentine ant is not in equilibrium with its environment and further expansions are expected into other urbanized areas, as well as natural habitats of the Costa Brava (as seen by Casellas (2004) at finer scales). As such, similarly to the whole Catalonia, it would be necessary to monitor the advancement of the invasion in order to determine the degree to which Argentine ant populations are established and spreading onto new non-invaded areas (Holway 1995).

On the other hand, considering the most influential environmental variables at regional and local scales, the inclusion of distance to the sea in both models and distance to urban areas in the local one seems to be highly conditioned by the history of the invasion. The hypothetical arrival of the Argentine ant through maritime commerce and subsequent jump dispersal associated to humans (Suarez et al. 2001) appears to be the most plausible hypothesis explaining the species occurrence along the coast and near those highly disturbed areas. As altitude per se does not seem to be a limiting factor for the species (Espadaler and Gómez 2003, Krushelnycky et al. 2005), its inclusion into both models is likely due to its correlation with distance to the sea: most of our occurrences are located near the coast, areas mainly dominated by low altitudes (Figure 7). On the other hand, previous studies (Holway et al. 2002b) demonstrated the influence of climatic factors, especially temperate climates and humidity, on the species distribution, which is reflected in the inclusion of precipitation in both models, and mean temperature and radiation in the local model. Thus, the inclusion of remote sensing data (EVI and NDVI) at both scales and the topographic position index at regional scales could probably explain why the Argentine ant prefers to occupy xeric environments near water courses (Holway 1998, Holway et al. 2002b).

In general, although ecological processes acquire new nuances when perceived from different spatial scales (Wiens 1989, Mackey and Lindenmayer 2001), the effects of changing scales on environmental variables do not seem evident from present results. However, it is important to remark the influence that the history of the invasion exerts in delineating Argentine ant distribution at landscape and local scales. Contrary to the general assumption that jump-dispersal is independent of the distance from the introduction focus, new populations of Argentine ants tend to cluster near the original populations forming a small sample of historically related populations at small spatial scales. Furthermore, another thing to notice is that the same predictor variable does not necessarily explain the same thing in both local and regional models. Changing the spatial scale of the analysis also changes the object of study (Farina and Belgrano 2004, Farina et al. 2005). As such, present niche models for the Argentine ant at regional scales could be somehow predicting those areas suitable for supercolonies, while local scale niche models would predict the specific conditions of each individual colony or nest.

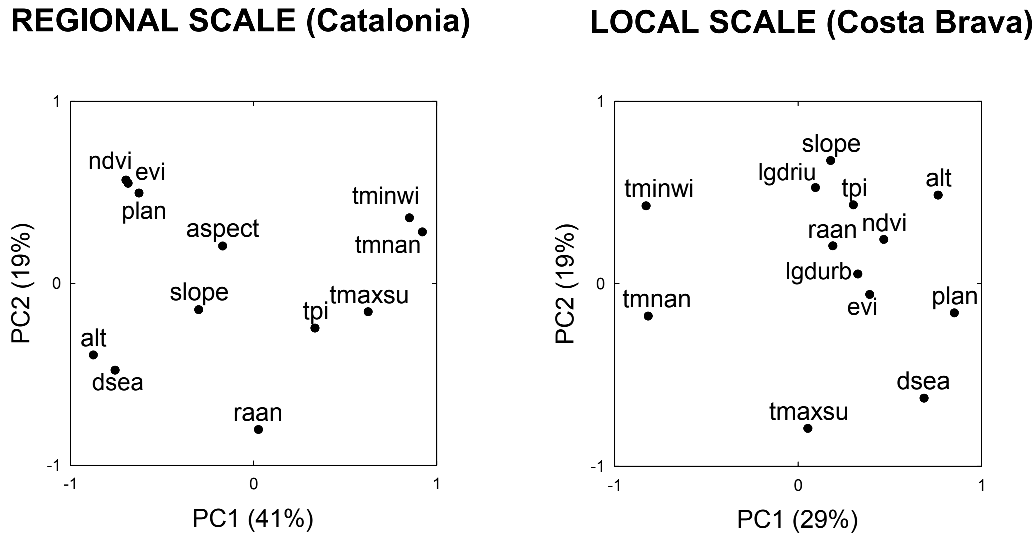

Figure 7 Visualizations of the environmental conditions at regional and local scales using Principal Components Analysis. The position of each variable is graphed onto a bivariate plot of the first two principal components. (See material and methods section for an explanation of abbreviations)

Question 2: Is Argentine ant invasion identical throughout the Costa Brava?

Occurrence data for the Costa Brava indicates that the species certainly has different distributional patterns along the coastal area of the Costa Brava. As mentioned in the first paragraph of the discussion, these differences among areas could be due principally to historical factors or ecological niche differences.

From a historical, or temporal, point of view, the Argentine ant was more likely to arrive first in the GC area than in other ones. Boats arriving from South America, and especially the Rio de la Plata region, arrived first at the main harbours in the GC area, and from there merchandises were delivered by boat or wheeled transport to the other areas of the Costa Brava (Barbaza 1988). Prior to their arrival in NE Iberian Peninsula, these boats from South America followed strategic transatlantic routes that curiously linked the main invaded areas of eastern America with the northeastern Iberian Peninsula (Fradera and Yáñez 1995). Although it is difficult to exactly corroborate this previous relationship and establish the exact date and place of the Argentine ant's arrival in the Costa Brava, the current species distribution (occurrence decreasing towards the northernmost coastal areas) seems to indicate that this hypothesis on the introduction of the Argentine ant in the northeastern area of the Iberian Peninsula is highly plausible.

From an ecological point of view, although models developed in each area and tested on the other areas (using the occurrence data from these areas) show low model performance, we cannot conclude that the species occupies different ecological niches along the Costa Brava without confirming the nature of absence occurrence data (whether they represent sites not suitable for the species, or sites where the species could possibly occur). If the Argentine ant invasion is not in equilibrium, as it seems, localities where the species is not known to occur nowadays can be further invaded. In this sense, visual inspections of the overall predicted distributions along the Costa Brava (Figure 3) represent different chronological sequences of the same invasion process (CC predicted areas are included in the RB predicted areas, which at the same time are again included in GC predictions) and seem to corroborate the influence of historical factors on the invasion.

Taking into account the most relevant environmental variables included in the models, the actual Argentine ant distribution near the coast is influenced by both climatic and human presence conditions (Holway et al. 2002b, Carpintero et al. 2004). During the survey sampling, most invaded localities were found in urban areas or in the areas surrounding of human constructions, stressing the influence of anthropogenic activities on the invasion expansion. I also wish to emphasize the importance of distance to water courses in RB and CC areas, possibly indicating somewhat less favourable conditions compared to the GC area for Argentine ant expansion (Holway 1998).

Question 3: Does the Argentine ant occupy different ecological niches in coastal and inland areas?

As indicated by occurrence data, Argentine ant distribution varies among coastal and inland areas of the Gavarres-Cadiretes massif. Variations among areas can likewise be due to historical factors or ecological niche divergences.

From a historical perspective, as before, the coastal area appears to be the first focus of the Argentine ant introduction, from where it started to spread associated to humans (Holway 1995, Suarez et al. 2001). Its widespread occurrence near the coast is related to the extended urbanization process, and possibly accelerated by disturbance regimes (such as fire, J. Bas personal observation) and anthropogenic activities which are quite frequent in the massif. A similar pattern occurs in the interior areas of the massif, where urban settlements and human activities act as a new invasion focus of the species (Carpintero et al. 2004). The relationship between the cork industries and the spread of the Argentine ant has not been confirmed so far, but it is extremely surprising how most invaded interior areas correspond to those areas where the cork industries play a major role (personal observation).

From an ecological point of view, although models generated in one area do not correctly predict the occurrence points of the other, we cannot conclude that the species occupies different ecological niches in both areas. The Argentine ant invasion in the Gavarres-Cadiretes massif is still expanding in both areas, so models generated in one area failed to predict the occurrence data of the other area because of the inclusion of false absence data for calibrating and testing the models. However, when considering the overall-based models, predicted distributions suggest a general further expansion of the species in the whole massif.

Taking into consideration the environmental data, we realize that coastal and interior invasive processes are influenced by different environmental data: while coastal Argentine ant occurrence is influenced by several environmental factors, the currently known interior distribution is only influenced by a few. These differences could be explained by the limited geographic distribution in interior areas, which are strongly influenced by distance to urban areas.

Conclusions

The use of generalized additive models for predicting Argentine ant potential distribution at regional and local scales appears to correctly predict the species occurrence in those areas used to calibrate the models. However, the application of a presence-absence modelling approach for predicting the geographical range of an invasive species not in equilibrium with its environment has intrinsic limitations due to the use of non-true absence data for calibrating the models (Fielding and Bell 1997, Guisan and Zimmermann 2000). It would be interesting to repeat the same analysis with presence-only methods (Elith et al. 2006, Pearce and Boyce 2006) in order to determine the potential geographic dimensions of the Argentine ant invasion more precisely. Nevertheless, the present results offer new insights into the study of the Argentine ant invasion in the northeastern Iberian Peninsula region, at the same time as it indicates those areas that should adopt preventive measures.

Overall, our results suggest that a further expansion of the species is highly probable on the northeastern side of the Iberian Peninsula (Catalonia). Special attention should also be paid to the Costa Brava, where the species seems to present highly suitable conditions along the whole coast and also in inland areas. Measures such as limiting the movement of material (like rubbish, vegetal material, cork oak wood, land, etc) far away from the original areas if it has not been previously disinfected, or reducing the water runoff near urban areas would considerably reduce the invasion spread (Holway and Suarez 2006).

From the research perspective, similar sampling and modelling practices on natural habitats, also at different spatial scales, would be necessary to determine the exact geographic dimensions of the Argentine ant invasion, and also those environmental factors limiting its spread (Menke and Holway 2006). In addition, the identification of clusters of related Argentine ant occurrences would allow researches to identify jump-dispersal events in relation to the original focus of the invasion, and therefore quantify and predict future areas of expansion at landscape and local scales via spatially-explicit models. Likewise, further historical and genetic analysis should be carried out to determine in great detail the history of the Argentine ant invasion. This information would enormously contribute to elucidate the factors responsible for its present distribution, and establish the best management practices to prevent the expansion of the Argentine ant invasion.

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Chapter 6

General discussion and final conclusions

CHAPTER 6

General discussion

The ecological niche models developed herein have provided new, valuable information about the geographical dimensions of the Argentine ant invasion, and a better understanding of biogeographic issues related to the species' distributional patterns. This PhD thesis thus attempts to take the first step towards an integrated and multi-scalar analysis of the Argentine ant (*Linepithema humile*) geographic distribution. With this aim in mind, in the following sections I assess current niche modeling practice and interpret final results from a global perspective, in order to finally provide new insights into the study and prevention of the invasion.

Suitability of the niche modeling framework

As mentioned in the Introduction (Chapter 1), ecological niche models suffer from a series of inherent limitations when predicting the potential distribution of invasive species (Peterson 2003). A better understanding of these constraints to niche models is therefore required to obtain reliable and applicable conclusions. Because specific restrictions to each modeling practice have already been detailed at the end of previous chapters (Chapter 2, 3, 4 and 5), here I briefly review the strengths and weaknesses of the overall modeling framework for characterizing Argentine ant distribution across spatial scales. Since the main objective is to assess the suitability of the present modeling exercise in a broad multi-scalar context, this section is structured following the most relevant factors determining a species' potential distribution (Soberón and Peterson 2005) and the hierarchical framework proposed by Pearson and Dawson (2003).

Among the factors affecting the performance of the niche models, there are those abiotic conditions that play a major role in determining species occurrence. The **abiotic factors** included as predictor variables (in the form of GIS coverages) in our models appear to be in concordance with the hierarchical modeling framework described in the Introduction (Chapter 1). Only topography (Chapter 2) and remote-sensing data (acting as surrogates of land-use information) (Chapter 2 and 3) are at the limit of their applicability at global and regional scales, where climatic variables seem to ultimately govern the distributional pattern of most species (Willis and Whittaker 2002). The selection of each specific environmental dataset was made according to the species' biological requirements and their availability in a GIS format. Probably, the addition of certain environmental variables -such as soil temperature, level of humidity, degree-days (as the total amount of temperature required for an organism to develop its life cycle), etc., now difficult to obtain at the required resolution-would significantly improve the accuracy of our final predictions if available in the future.

Another factor is **biotic interactions** among Argentine ant and other species, both ant fauna and other animal species. It is, however, important to distinguish between native and invaded ranges, since Argentine ant populations face different biotic environments in different areas (see Chapter 1 and 3 for more details). According to previous studies (Heller 2004, Holway and Suarez 2004), biotic interactions only seem to limit Argentine ant distribution in the native area (through intraspecific competition among different colonies of *L. humile*, and through interspecific competition against other species) and in those introduced ranges with other widespread invasive ants (such as *Solenopsis invicta* in North America) (Wilson 1951). In the Iberian Peninsula, only the invasive *Lasius neglectus* could be a dangerous rival, but its restricted distribution barely affects the Argentine ant range at present (Espadaler and Collingwood 2000). Moreover, although intraspecific competition among introduced colonies of the Argentine ant could also limit its invasive potential to some extent (Giraud et al. 2002, Buczkowski et al. 2004), we suspect that such an aggressive behavior has a reduced influence within its introduced ranges and thus does not represent a major problem for our current predictions.

Taking these premises into consideration, biotic interactions may potentially influence those models based on native and North American occurrences (Chapter 2 and 3), but not those analyses performed within the Iberian Peninsula (Chapter 4 and 5). Nonetheless, given the predictive ability of models developed in the native area (Chapter 2) and among regions (Chapter 3), biotic interactions can probably have a limited influence in our study areas at broad spatial scales. Indeed, this statement is in concordance with the hierarchical framework (Pearson and Dawson 2003), which suggests that biotic interactions tend to affect niche models at fine scales. However, in relation to the worldwide distribution of the Argentine ant, it would be highly interesting to elucidate the influence of tropical versus subtropical/mediterranean biotic interaction on the invasion. The most highly invaded regions at present are outside the tropics, but we do not know whether this is due to different sampling efforts or to the effects of a stronger interspecific competition among ants in the tropics.

Indeed, the major constraints to predicting the invasive potential of the Argentine ant are related to **species dispersal**. These limitations are not due to biological characteristics of the species or the existence of geographic barriers, but to the history of the invasion (see Chapter 1). Despite its widespread distribution around the world, the Argentine ant is not known to be in equilibrium with its environment and further expansions are still expected in its introduced ranges (Chapters 2, 3, 4 and 5). This non-equilibrium situation is a drawback for most niche models, since these implicitly assume a state of equilibrium between the species and its environment (Guisan and Zimmermann 2000). From a statistical perspective, it supposes the inclusion of false absence data (localities suitable for the species but still not invaded) and a reduced set of presences in our modeling exercise to calibrate and evaluate the final models. As such, models derived from this set of occurrence data may underestimate the potential geographic range of the species. This limitation is less restrictive for large-scale predictions based on the native distributional area of the species (Chapter 2 and 3), but local-scale models (Chapter 4 and 5) have difficulties to cope with this non-equilibrium state (Guisan and Zimmermann 2000, Peterson 2005).

Finally, as hinted at three paragraphs above, **changes on phenotypic and genetic characteristics** of Argentine ant populations after introduction could influence their invasive success (Chapter 1). However, possible changes in tolerance to environmental conditions, which could facilitate its persistence outside the optimum native environment, do not seem to be responsible for the success of the Argentine ant, at least at global and regional spatial scales (Chapter 3). This finding of similar ecological niche characteristics of Argentine ants among distributional areas may actually reflect the maintenance of the social structure between both native and introduced populations, where favorable ecological conditions would have allowed the species to largely increase the size of introduced supercolonies and become a better competitor in new invaded areas (Pedersen et al. 2006). However, due to the lack of studies at local scales searching for changes in Argentine ant environmental tolerances, we cannot underestimate their influence. More research on this topic is necessary to clarify the influence of phenotypic and genetic changes in the Argentine ant native distribution and its expansion into novel environments.

The above-mentioned constraints have to be taken cautiously when interpreting final results in order to produce reliable conclusions, especially when predicting the potential impacts of climate change on Argentine ant distribution (Pearson and Dawson 2003) or when adopting a cross-prediction analysis among different regions (Thuiller et al. 2004). There is no perfect modeling approach that captures the infinite complexity of natural environments or the multi-processes that determine a species' geographic distribution, but the choice of the most appropriate technique in each specific modeling context may reduce the artefacts due to previous restrictions (Elith et al. 2006). Additionally, the adoption of a multiscalar design (both in the sampling and modeling procedures) from the beginning would have allowed bridging the gap between predictions across spatial scales, and provide a new framework for the study of the Argentine ant invasion. Certainly, the current increase in the number of papers devoted to methodological aspects of niche models and in the tools available for modeling species distribution across spatial scales (Guisan and Thuiller 2005) will significantly improve final predictions. In this sense, previous to the finalisation of this PhD thesis, some modelling studies that complemented and extended the results of herein developed niche models have appeared (Krushelnycky et al. 2005, Hartley et al. 2006). However, the merit of the herein developed niche models is to provide the first quantitative approximation to Argentine ant geographic distribution as well as a valuable tool for establishing management strategies to control and prevent the invasion (Peterson 2003).

Argentine ant invasion across spatial scales

After elucidating the strength and weakness of the present niche modeling framework, this section focuses on the emergent ecological characteristics of Argentine ant invasion across spatial scales. Thus, in the next paragraphs I briefly summarize the most striking points of the previous analyses and emphasize those novel properties derived from a cross-analysis of our results at several spatial scales.

In general, our results suggest that the Argentine ant can undergo further expansions worldwide (Chapter 2), and at regional and local scales (Chapter 4 and 5). Areas near the coast and following the main rivers are predicted as highly suitable for the species (Chapter 2, 3 and 4). These predictions are in concordance with the currently known occurrence of the species, which has a peripheral distribution along coastal areas worldwide, but further areas without confirmed presence of the species are still expected to become invaded according to present-day environmental conditions (Chapter 2, 3, 4 and 5). These results give additional support to the idea that the Argentine ant is not currently in equilibrium with its environment as also indicated by other studies around the world (Casellas 2004, Krushelnycky et al. 2005).

As already mentioned in previous paragraphs, this non-equilibrium state poses a major question to our results: do those models developed based on occurrence data from the introduced range (Chapter 3, 4 and 5) reflect the entire geographic potential of the invasion? Literature on the Argentine ant states that its distribution is highly constrained by temperature and water availability, and it avoids colder inland areas in the absence of human intervention (Holway 1998). However, restricting Argentine ant distribution near coastal regions with a temperate climate needs further examination. Our results cannot confirm this statement. On the contrary, predictions at global and regional scales (Chapter 2 and 3) suggest some inland areas, though to be unsuitable for the species, as also suitable. In this respect, further research is necessary to determine if the current distribution of the Argentine ant is more likely to be due to the history of the invasion (in which seaports are the major ports of entrance) or to real limitations in its tolerance to environmental conditions. Special attention needs to be paid to those invaded localities with extreme environmental conditions, such as the interior of the Iberian Peninsula (Espadaler and Gómez 2003) and most inland areas in North America (Suarez et al. 2001) among others.

In the Iberian Peninsula, this peripheral distribution is suggested by both occurrence data and predicted distribution at regional and local scales (Chapter 4 and 5). However, this coincidence is certainly not surprising since predictions within the Iberian Peninsula have been developed using occurrence from the same area. On the contrary, if we take a look at those projections from the native to the Iberian Peninsula, based on the equilibrium situation of native occurrences (Peterson 2005) and niche conservatism of the Argentine ant at regional scales (Chapter 3), regional models also predict some inland areas with extreme environmental conditions as suitable for the species (Chapter 3). Thus, further research is needed to assess the real environmental tolerance of the Argentine ant to those supposedly non-suitable environmental conditions.

Focusing our attention on the northeastern side of the Iberian Peninsula, models at local scales (Chapter 5) also suggest the same peripheral distribution near the coast as that previously described for models developed in the Iberian Peninsula at regional scales (Chapter 4). However, these finer-scale projections for Argentine ant distribution seem more constrained by distance to the sea than previous results at broader scales (Chapter 2 and 3). Models at finer spatial scales (with high resolutions) tend to adjust predictions more closely to Argentine ant occurrence data than models at broad scales, somewhat reflecting the influence that the history of the invasion exerts at finer scales. This becomes evident when comparing Catalonia and Costa Brava models (Chapter 5): regional models predict further suitable areas for the Argentine ant than local models, probably due to the inclusion of a great proportion of false absence data to calibrate niche models at finer spatial scales. Differences between predictions on Argentine ant distribution across spatial scales depend to a great extent on the occurrence data set used to develop the models. Thus, it is important to notice that occurrences also need to be scaled according to the objectives of the study.

As such, even though I only referred to present-day predictions in previous paragraphs, the effects of climate change on the geographic distribution of the Argentine ant also need further considerations from a multi-scalar context. According to our results (Chapter 2), the Argentine ant is expected to expand its environmental range to higher northern and southern latitudes, and retract in the tropics at global spatial scales. However, since the extent to which species are able to achieve large-scale migrations is still poorly understood and models did not take species' dispersal capacity to migrate into account, the impacts of climate change on the Argentine ant invasion at global scale remain incertain to some extent (Broenniman et al. 2006). Specific knowledge on the dispersal ability of *L. humile* to migrate would be necessary to improve the ecological realism of our predictions, by incorporating explicitly migration rates into our models. Furthermore, the consequences of future climates on the Argentine ant invasion remain absolutely uncertain, and therefore less predictable, at local scales (Sala et al. 2000). *L. humile* presence is extremely influenced by climatic conditions and water presence (Holway 1998), so a better understanding of how these drivers will change in the future at local scales is required to predict the real effects of climate change on the invasion pattern. Special attention needs to be paid to riparian habitats, natural corridors that favor the spread of the Argentine ant into novel environments, which are also indicated as extremely vulnerable and may experience large biodiversity losses (Sala et al. 2000).

As an additional final remark, we will address the more general context of widespread ant invasions and our ability to elucidate common patterns among them. Comparing the Argentine ant potential distribution at global scales with the red imported fire ant (*Solenopsis invicta* Buren) recently modeled by (Morrison et al. 2004), we realize that there are some similar patterns among predicted areas. These similarities between both invasions suggest the possible existence of common ecological niche attributes among worldwide ant invasions (Lester 2005), in addition to morphological and life history characteristics and the tendency to occupy human-disturbed habitats (Hölldobler and Wilson 1990, Passera 1994, McGlynn 1999, Holway et al. 2002, Tsutsui and Suarez 2003). As such, according to studies on behavior and functional group classification for predicting the establishment of transferred ants (McGlynn 1999), it would be highly interesting to puzzle out if widespread invasive ants have similar ecological niches worldwide. This knowledge will certainly give us a better understanding of the invasiveness of ant species and would facilitate the monitoring of those areas most susceptible to being invaded by some groups of ants and enhance the effectiveness of preventive measures to control ant invasions (Mack et al. 2000).

Which direction to follow according to previous results?

In this context, future research efforts should be made to improve current knowledge on the spatial distribution of the Argentine ant invasion. First of all, there is an urgent need to set up worldwide distributional database on the Argentine ant, which could be updated and continuously maintained to notify new and/or predicted occurrences (both presence and absence) of the species. This would enormously help to monitor the invasion spread from spatial and temporal points of view, with a minimum effort since most of the current occurrence data have already been summarized in a few works (see Chapter 2).

Secondly, more studies determining the influence of factors (both abiotic and biotic factors, species dispersal, and phenotypic and genotypic changes) governing the spread of the Argentine ant are needed in different areas and across spatial scales, in order to expand the actual knowledge of the species (see Chapter 1 for a brief description of the current work on it). Some indications have already been presented in each chapter, and also in the above sections. In general, however, the most interesting topics at broader scales would be: analyzing the genetics of Argentine ant populations (to elucidate their origin, and thus determine possible changes after introductions and the population-specific mechanisms of dispersal) and the biotic restrictions in each introduced area. Likewise, at local scales, more single-site studies at the invasion front (by establishing a multiscale nested sampling strategy along the main environmental gradients or a long-term monitoring of an invasion focus) could significantly contribute to defining the invasive pattern in detail.

Finally, from the niche modeling perspective, the adoption of a mechanistic approach combining physiological data with the species' dispersal capabilities would allow to test several hypotheses about its expansion at landscape and local scales. In addition to Argentine ant' characteristics, these models also take into account the environmental heterogeneity of the landscapes. The use of such spatially-explicit models incorporating the species' dispersal ability in relation to landscape characteristics would allow tracking the migration and gene flow among populations, and thereby determining the ecological and genetic viability of the Argentine ant in introduced areas. The combination of niche modeling and landscape ecology is thus required to produce more realistic distributional patterns of Argentine ant invasion across spatial scales.

Nevertheless, it is worth remembering that one of the main, if not the last, objectives underlying distributional studies of invasive species is to elucidate the geographic dimension of the process, which is required to establish efficient management strategies for preventing further expansions of the invasion. As such, considerable efforts should be made with those human activities susceptible to transporting propagules of Argentine ant over long and short distances, from the native area or from another introduction focus. These activities include: rubbish, debris and land movements; cork industries; farming-related practices; urbanization processes; vehicle access, etc. Effectively controlling these secondary jump-dispersion events is crucial for avoiding the spread of the Argentine ant into natural habitats and ecosystems through a diffusion process (Krushelnycky et al. 2005), which seems to be highly probable in all neighboring areas near human settlements (Carpintero et al. 2004). Once introduced into urban areas, some measures (such as avoiding water runoff or movement of infested material) can also be adopted to mitigate the spread of Argentine ant.

All measures aimed at preventing and controlling Argentine ant invasion, however, need to be integrated into a global strategy acting across several temporal and spatial scales, such as those suggested by McNeely et al. (2001). But global and regional initiatives will not successfully manage the complex phenomenon of invasions without the widespread support of all citizens (Vitousek et al. 1997), who can contribute to preventing or mitigating them by becoming more aware of those local actions that favor the spread of invasive species.

Final conclusions

Understanding the geographical dimension of the Argentine ant invasion is extremely important to establish efficient management strategies for preventing and controlling the invasion spread at different spatial scales. In the absence of detailed occurrence data, ecological niche models help us to estimate the potential invasiveness range of the species. As such, in this PhD thesis we modeled Argentine ant ecological niches to identify areas susceptible to becoming invaded in the present and in concordance with future climate change, at the same time as we also elucidated the influence of several environmental processes underlying these distributional patterns.

The most relevant conclusions obtained from our analysis at several spatial scales are:

1. Ecological niche models appeared as valuable tools for predicting Argentine ant potential geographic distribution at different spatial scales, at the same as they allowed us to test different hypotheses (such as future distribution according to climate change, comparisons between native and invaded ecological niches, and also differences in the species' distributional patterns in different areas) and determine those areas that should be vigilant against the introduction of the species.

2. At global scales, the Argentine ant is expected to occupy a broader distribution in its native and worldwide invaded ranges than is currently appreciated. Particularly important are susceptible areas where few or no records of Argentine ants are known, particularly northern South America and the Caribbean, parts of the Mediterranean, eastern Europe, tropical coastal Africa, Madagascar, Southeast Asia, India, China, northern Australia and many oceanic islands.

3. In relation to global warming, our predictions at global scales suggest a general reduction of potential distribution areas worldwide for *L. humile*, particularly in the tropics. However, some higher latitude areas are predicted to become more suitable for invasion (East Asia, northeastern United States, broader areas around the Mediterranean and Caspian Seas, southern Africa, and southern Australia).

4. The ecological niche of Argentine ants is not markedly different among native and invaded (United States of America, Japan, and Iberian Peninsula) areas, suggesting that ecological, behavioral, and genetic differences occurring after introduction observed in detailed single-site studies are not manifested at regional spatial scales.

5. At regional scales, although the Argentine ant also presents similar ecological niches at western and eastern Iberian Peninsula, small divergences between both areas suggest that the western invasion process occupies a slighter wide range of environmental characteristics than in the East. Overall, further expansion of the species is still possible along the coastal areas and major river courses (such as the Ebro, Guadalquivir, Guadiana and Tajo rivers) in the Iberian Peninsula.

6. At local scales, a further expansion of the species is highly probable on the northeastern side of the Iberian Peninsula (Catalonia). Special attention should also be placed on the Costa Brava, where the species seems to present highly suitable conditions along the whole coast and also in inland urbanized areas.

7. Further field work and modeling practices at broad and fine scales should be done in order to exactly determine the present day geographic distribution of the Argentine ant, since it would enormously improve our assessment of the real invasive potential of the Argentine ant and determine new sites vulnerable to invasion where preventive measures should be taken.

I hope this contribution helps to increase the awareness of our society, and principally our politicians, regarding the importance of establishing efficient management measures to avoid the Earth’s biodiversity losses caused by biological invasions, which is ultimately the main consequence of our highly widespread and invasive anthropocentric perception of the Earth.

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ANNEXES

Annexe 1 Occurrence data of Argentine Ant (*Linepithem humile*) around the world in geographic coordinates. The first column refers to presence (P) or absence (A) of the species, and presences from the considered native area are indicated with (*). Data has been obtained from museum and personal collections, and scientific literature (Annexe 2).

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
Argentina			
P	Chubut, Rawson	-65,100	-43,300
P	Chubut, 3km N Puerto Lobos	-65,100	-41,973
P*	Santa Fe, Rosario	-60,683	-32,917
P*	Santa Fe, Rosario	-60,667	-32,950
P*	Entre Ríos, P. N. Pre Delta	-60,659	-32,965
P*	Entre Ríos, Diamante	-60,647	-32,016
P*	Santa Fe, main road between Paraná and Santa Fe	-60,572	-31,677
P*	Santa Fe, Fives Lille	-60,350	-30,150
P*	Entre Ríos, Victoria	-60,167	-32,635
P*	Entre Rios, Paraná, Estación Sosa	-60,000	-31,667
P*	Entre Rios, Paraná, Estación Sosa	-59,917	-31,733
P*	Entre Ríos, Gualeguay	-59,333	-33,150
P*	Santa Fe, Porto Ocampo	-59,265	-28,498
P*	Lima, Zárete	-59,200	-34,050
P*	Entre Rios, Port Ibicuy	-59,167	-33,800
P*	Buenos Aires, Zárate	-59,018	-34,103
P*	Entre Ríos, Villaguay	-59,017	-31,850
P*	Buenos Aires, Rosas F. C. Sud	-58,933	-35,967
P*	Buenos Aires, Campana	-58,931	-34,199
P*	Buenos Aires, R. Otamendi	-58,901	-34,219
P*	Buenos Aires, R. Otamendi	-58,900	-34,233
P*	Entre Ríos, 10km S Medanos	-58,867	-33,480
P*	Chaco, Resistencia	-58,867	-27,430
P*	Corrientes, Corrientes	-58,833	-27,467
P*	Corrientes, Paseo de la Patria	-58,573	-27,318
P*	Olivos	-58,500	-34,517
P*	Buenos Aires, Vicente López	-58,471	-34,526
P*	Buenos Aires, Buenos Aires	-58,467	-34,600
P*	Buenos Aires, R. Costanera Sur	-58,356	-34,116
P*	Buenos Aires, Buenos Aires	-58,350	-34,633
P*	Formosa, Herradura	-58,283	-26,517
P*	Buenos Aires, Isla Martín García	-58,267	-34,350
P*	Entre Ríos, P. N. El Palmar	-58,209	-31,875
P*	Formosa, Formosa	-58,183	-26,183
P*	Entre Ríos, Colon	-58,117	-32,233
P*	Formosa, Mojón de Fierro	-58,050	-26,050
P*	Buenos Aires, La Plata	-57,950	-34,933
P*	Formosa, Clorinda	-57,717	-25,283
P*	Formosa, Puerto Pilcomayo	-57,653	-25,368
P*	Monte Caseros	-57,630	-30,244
P*	Corrientes, Ita Ibate	-57,167	-27,417
P*	Corrientes, Alvear	-56,552	-29,110
P*	Corrientes, Alvear, Port Alvear	-56,550	-29,100
P*	Corrientes, Sto. Tomé	-56,050	-28,550
P*	Misiones, Posadas	-55,883	-27,383
A	Misiones, P. N. Iguazú	-54,436	-25,703
P*	Misiones, P. N. Iguazú	-54,433	-25,700
Australia			
P	Western Australia, Herdsman Lake	115,800	-31,917
P	Western Australia, Perth	115,833	-31,933
P	Western Australia, Albany	117,892	-35,017
P	Western Australia, Esperance	121,900	-33,867
P	Adelaide	138,600	-34,933
P	Victoria, Swan Hill	143,567	-35,350
P	Melbourne	144,967	-37,817
P	Victoria, 12km W Wangaratta	146,200	-36,367
P	Tasmania, Launceston	147,167	-41,450
P	Tasmania, Hobart	147,333	-42,917
P	New South Wales, Sydney	151,217	-33,883
Belgium			
P	Bruxelles, Jardin Botanico	4,333	50,833
Bermuda			
P	Wreck Hill	-64,886	32,280
P	Cedar Hill	-64,864	32,252
P	Southampton Parish	-64,856	32,251

Pres Lh	City/ Town/ Place	Longitude	Latitude
P	Hamilton	-64,784	32,294
P	Dockyards	-64,783	31,300
P	Paget	-64,782	32,278
P	Bermuda,	-64,750	32,300
P	Harrington Hundreds	-64,729	32,319
P	Knapton Hill	-64,723	32,317
P	Harrington Sound	-64,722	32,331
P	Leamington Caves	-64,709	32,343
P	Mullet Bay	-64,693	32,375
P	Saint David's Head	-64,633	32,367
Brazil			
P	Amazonas, Manaus	-60,033	-3,117
A	Mato Grosso, Utiariti, Rio Papagaio	-58,283	-13,033
P*	Mato Grosso do Sul, Pto. Murtinho	-57,867	-21,700
P*	Mato Grosso do Sul, Corumbá, Faz. Sta. Blanca.	-57,650	-19,017
P*	Mato Grosso do Sul, Corumbá, Pto. Esperança	-57,450	-19,617
P*	Mato Grosso do Sul, Passo do Lontra	-57,017	-19,583
P*	Mato Grosso do Sul, Passo do Lontra	-57,017	-19,567
P	Rio Grande do Sul, N. Würtemberg	-53,500	-28,300
A	Santa Catarina, N. Teutónia	-52,383	-27,183
P	Rio Grande do Su, Pelotas	-52,333	-31,767
A	Rio de Janeiro, Maringá, Poço das Antas	-52,000	-23,400
A	Paraná, Rio Negro	-49,800	-26,100
A	Santa Catarina, Blumenau	-49,050	-26,933
A	São Paulo, Agudos	-49,000	-22,467
P	Goiás, Anapolis	-48,967	-16,333
A	Santa Catarina, Gaspar	-48,950	-26,933
A	São Paulo, Lençois, Pta.	-48,783	-22,600
A	São Paulo, Anhembi, Faz B. Rico	-48,117	-22,800
A	Goiás, Alto Paraiso, Faz Bona Espera	-47,517	-14,117
A	São Paulo, Cajurú, Fazenda Santa Carlota	-47,300	-21,283
A	São Paulo, Genebra	-47,100	-22,817
A	São Paulo, Barueri	-46,883	-23,350
A	São Paulo, Sao Paulo	-46,617	-23,717
A	São Paulo, Alto da Serra	-46,317	-23,783
A	São Paulo, Salesopolis, Est. Biol. Boraceia	-45,900	-23,650
A	São Paulo, Campos do Jordão	-45,583	-22,733
A	São Paulo, S. Sebastião, B. S. Fancisco	-45,417	-23,800
A	São Paulo, Caraguatatuba, Res. Flor.	-45,417	-23,617
A	São Paulo, Guarantingueta	-45,217	-22,817
A	São Paulo, Ilha dos Buzios	-45,133	-23,800
A	São Paulo, Cunha, P. E. Serra do Mar	-45,007	-23,251
P	Minas Gerais, Sete Lagoas	-44,233	-19,450
A	Minas Gerais, Serra Caraça	-43,500	-20,133
A	Rio de Janeiro, Floresta de Tijuca	-43,283	-22,933
P	Rio de Janeiro, Rio de Janeiro	-43,233	-22,900
A	Rio de Janeiro, Petropolis	-43,167	-22,517
P	Minas Gerais, Viçosa, Cafezal	-42,883	-20,750
A	Espírito Santo, Santa Tereza	-40,600	-19,917
A	Espírito Santo, Pedro Canario, Conc. de Barra	-39,750	-18,583
Cameroon			
P	Centre-Sud, Nkoemvom	11,133	2,800
Chile			
P	Arauco	-73,317	-37,250
P	Malleco, Sierra Nahuelbuta	-73,217	-38,017
P	Magallones, 4km W Laguna Amarga	-72,450	-50,590
P	Aisen, 8km W Chile Chico	-71,838	-46,550
P	Coquimbo, P. N. Fray Jorge	-71,667	-30,667
P	Valpariso, Plaza Victoria	-71,601	-33,048
P	Quintero	-71,533	-32,783
P	Valparaiso, 10km E Viña del Mar	-71,517	-33,008
P	Puchuncavi	-71,412	-32,728
P	Santiago de Chile, Parque Forestal	-70,667	-33,450
P	Santiago, Questrada de la Plata	-70,550	-33,300
P	Maipu, La Rinconada	-70,470	-33,310

Pres Lh	City/ Town/ Place	Longitude	Latitude
Colombia			
P	Quindio, Armenia	-75,700	4,500
P	Medellin	-75,536	-6,291
P	Meta, la Macarena, Reserva	-73,900	2,183
Easter Island			
P	Kau Ranu Crater	-109,450	-27,150
P	Hanga roa	-109,433	-27,150
Ecuador			
P	Pichincha, Mitad del Mundo	-78,456	-0,002
P	Pichincha, Carapungo	-78,449	-0,088
El Salvador			
P	Quezaltepeque	-89,271	13,833
France			
P	Grâce	-1,933	47,483
P	Maurès	0,817	44,683
P	Toulouse	1,433	43,600
P	Port-Leucate	3,033	42,917
P	Sète	3,683	43,400
P	Montpellier	3,883	43,600
P	La Grande Motte	4,083	43,567
P	Martigues	5,050	43,400
P	La Ciotat	5,600	43,167
P	Tamaris	5,900	43,083
P	Toulon	5,933	43,117
P	Provence-Alpes-Côte D'Azur, Hyères	6,117	43,117
P	Le Lavandou	6,367	43,133
P	Provence-Alpes-Côte D'Azur, Castellane	6,517	43,850
P	Provence Alpes Côte D'Azur, Ste. Maxime	6,633	43,300
P	Saint-Aygulf	6,733	43,383
P	Callian	6,750	43,633
P	Saint Raphael	6,767	43,417
P	Esterel	6,817	43,533
P	St. Jean de Cannes	6,877	43,523
P	Mandelieu	6,933	43,550
P	Mougins	7,000	43,600
P	Provence-Alpes-Cote d'Azur, Cannes	7,017	43,550
P	Iles de Lérins	7,050	43,517
P	Vence	7,117	43,717
P	Antibes	7,117	43,583
P	Étang de Vaugrenier	7,133	43,633
P	Barsur-Loup	7,150	43,633
P	Nice	7,250	43,700
P	Menton	7,500	43,783
P	Calvi	8,750	42,567
Germany			
P	Hamburg	9,817	54,133
P	Berlin, Botanical Garden	13,333	52,500
Italy			
P	Liguria, San Remo	7,767	43,817
P	Genoa	7,950	44,417
P	Alassio	8,167	44,000
P	Celle Ligure	8,550	44,333
P	Varazze, Savona	8,633	44,367
P	Genoa	8,950	44,417
P	Nervi	9,033	44,383
P	Monéglia	9,500	44,233
P	Toscana, Monte Argentario Giannella	11,167	42,417
P	Toscana, Orbetello, Faniglia	11,217	42,450
P	Rome	12,483	41,900
P	Sicilia, Palermo	13,367	38,117
P	Campania, Naples	14,250	40,833
Japan			
P	Chugoku, Yamaguchi	131,483	34,167
P	Yanai	132,100	33,983
P	Iwakuni	132,200	34,100
P	Iwakuni	132,233	34,167

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	Hatsukaichi	132,333	34,350
P	Itsukaichi	132,367	34,350
P	Dejima	132,450	34,350
P	Ujina	132,467	34,350
P	Onaga	132,500	34,400
P	Fuchu	132,517	34,383
P	Hiroshima, Yokkaichi	133,333	34,767
P	Chugoku, Kobe	135,167	34,683
P	Kobe	135,183	34,667
Lesotho			
P	Maseru, Maseru	27,483	-29,317
Mexico			
P	Baja California, Ensenada, Cortera FR	-116,626	31,861
P	Baja California, 3.5mi WNW Catavina	-115,004	29,886
P	Baja California, Todos Santos	-114,750	29,500
P	Baja California, Guerro Negro	-114,057	27,961
P	Mexico City, Univesity Campus	-99,139	19,434
P	Distrito Federal, México	-99,133	19,433
Monaco			
P	Monaco	7,417	43,733
Morocco			
P	Tangier, Tangier	-5,817	35,783
Namib			
P	Erongo, Swakopmund	14,533	-22,683
P	Swakopmund	14,533	-22,650
New Zealand			
P	Kaitaia	171,250	-42,467
P	Mt. Smart	171,300	-42,700
P	Christchurch	172,633	-43,533
P	Port Nelson	173,267	-41,267
P	Nelson	173,283	-41,283
P	Dargaville	173,883	-35,933
P	Piha	174,467	-36,950
P	Te Atatu	174,650	-36,833
P	Warkworth	174,667	-36,400
P	Hauraki Gulf	174,740	-36,400
P	Kelburn	174,767	-41,283
P	Auckland	174,767	-36,867
P	Whangaparaoa	174,767	-36,633
P	Wellington	174,783	-41,300
P	Petone	174,883	-41,233
P	Lower Hutt	174,917	-41,217
P	Hamilton	175,283	-37,783
P	Morrinsville	175,533	-37,650
P	Tauranga Harbour	176,020	-37,640
P	Mt Maunganui	176,167	-37,617
P	Hastings	176,833	-39,650
P	Bay of Penty	177,000	-37,950
Paraguay			
A	Boqueron, P. N. Tte. Enciso	-61,667	-21,200
P*	Boqueron, P. N. Defensores del Chaco, Cerro León	-60,333	-20,417
P*	Pte. Hayes, 5km SE Pozo Colorado	-58,764	-23,552
P*	Neembucu , Pilar	-58,300	-26,867
P*	Central, Asunción	-57,817	-25,267
P*	Ñeembucu,	-57,784	-26,868
P*	Central, Asunción	-57,667	-25,267
P*	Pte. Hayes, Villa Hayes	-57,567	-25,100
P*	Pte. Hayes, Benjamín Aceval	-57,567	-24,967
P*	Pte. Hayes, Rio Confuso, Ruta trans-chaco	-57,550	-25,100
P*	Central, San Lorenzo	-57,517	-25,333
P*	Pte. Hayes, Rt. 5 across from Concepción	-57,458	-23,455
P*	Cordillera, San Bernadino	-57,317	-25,267
A	Cordillera, Caacupé, Camp. J. Norment.	-57,083	-25,367
P*	San Pedro, Pto. Rosario.	-57,000	-24,500
A	Canindeyú, Reserva Natural del Bosque Mbaracayú	-55,533	-24,133

Pres Lh	City/ Town/ Place	Longitude	Latitude
Peru			
P	Lima, Los Condores	-77,050	-12,050
P	Lima	-71,600	-15,683
Poland			
P	Dolnoslaskie, Breslau	17,033	51,100
Portugal			
P	Azores, Sao Jorge	-28,050	38,633
P	Madeira, Porto Santo Calheta	-17,200	32,700
P	Madeira, Porto Moniz	-17,167	32,850
P	Madeira, Ribeira Brava	-17,067	32,650
P	Madeira, São Vicente	-17,050	32,800
P	Madeira, Caramujo	-16,933	32,767
P	Madeira, Funchal, Praia Formosa, Funchal	-16,900	32,633
P	Madeira, Vale de Paraiso	-16,867	32,667
P	Madeira, Porto da Cruz	-16,833	32,767
P	Madeira, Ilheu Chão	-16,533	32,583
P	Madeira, Porto Santo, Serra de dentro- Juliana	-16,333	33,067
P	Lisboa, Praia das Macas	-9,467	38,817
P	Cascais	-9,430	38,702
P	Lisboa, Cascais	-9,417	38,700
P	Lisboa, Estoril	-9,400	38,700
P	Sintra-Estremadura	-9,372	38,797
P	Lisboa, Mafra	-9,333	38,933
P	Mafra	-9,330	38,928
P	Lourinha	-9,313	39,238
P	Oeiras	-9,307	38,683
P	Torres Vedras	-9,255	39,092
P	Peniche	-9,252	39,355
P	Tapada da Ajuda (ISA)	-9,212	38,710
P	Montemor	-9,200	38,817
P	Almuda	-9,157	38,675
P	Sobral do Monte Agraco	-9,157	39,008
P	Bombanal	-9,150	39,258
P	Loures	-9,148	38,828
P	Lisboa, Lisboa, Parque Florestal de Monsanto	-9,133	38,717
P	Quinta do Furadouro (CELBI)	-9,127	39,393
P	Caldas da Rainha	-9,127	39,407
P	Sesimbra	-9,107	38,447
P	Cadaval	-9,092	39,240
P	Acruda dos Vinhos	-9,072	38,982
P	Nazaré	-9,057	39,595
P	Barreiro	-9,047	38,648
P	Mata da Machada (SFN)	-9,028	38,622
P	Alenquer	-9,010	39,057
P	Arrabida-Extremadura	-9,000	38,465
P	Vilafranca de Xira	-9,000	38,938
P	Moita	-8,993	38,648
P	Alcobaca	-8,977	39,543
P	Montijo	-8,965	38,692
P	Rio Maior	-8,930	39,342
P	Vila do Bispo	-8,913	37,078
P	Zona de Tróia (Setúbal)	-8,890	38,482
P	Setúbal	-8,888	38,525
P	Samora correia	-8,860	38,939
P	Sires	-8,860	37,960
P	Azambuja	-8,860	39,070
P	Palmela	-8,853	38,572
P	Figueira da Foz	-8,850	40,157
P	Nazaré	-8,840	39,758
P	Esposende	-8,825	41,523
P	Viana do Castelo	-8,825	41,708
P	Caminha	-8,825	41,900
P	Batalha	-8,818	39,657
P	Aljezur	-8,802	37,297
P	Benavente	-8,802	38,977
P	Porto de Mós	-8,802	39,595

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	Cartaxo	-8,790	39,167
P	Sesimbra	-8,790	37,720
P	Esposende	-8,787	41,540
P	Salvaterra de Magos	-8,783	39,027
P	Barra	-8,748	40,643
P	Póvoa de Varzim	-8,740	41,350
P	Vila do Conde	-8,737	41,345
P	Faro, Algarve, Luz nr. Lagos	-8,733	37,083
P	Mira	-8,725	40,428
P	VilaNova de Cerveira	-8,723	41,938
P	Porto, Leca de Palmeira	-8,700	41,200
P	Santiago de Cacém	-8,697	38,017
P	Matosinhos	-8,692	41,227
P	Santarem	-8,683	39,233
P	Vagos	-8,678	40,552
P	Lagos	-8,673	37,110
P	Santarém	-8,672	39,233
P	Zona de Pegoes-Gare	-8,660	38,665
P	Ilhavo	-8,660	40,600
P	Pegoes	-8,643	38,673
P	Aveiro	-8,642	40,635
P	Espinho	-8,642	41,008
P	Murtosa	-8,630	40,737
P	Almeirim	-8,627	39,210
P	Soure	-8,625	40,060
P	Maia	-8,625	41,218
P	Valenca	-8,625	42,028
P	Porto, Oporto	-8,617	41,150
P	Barcelos	-8,613	41,537
P	Vila Nova de Gaia	-8,612	41,178
P	Oporto	-8,603	41,160
P	Ovar	-8,595	40,863
P	Ponte de Lima	-8,595	41,790

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	Cantanhede	-8,588	40,345
P	Alpiarca	-8,580	39,258
P	Estaneja	-8,565	40,758
P	Grandola	-8,557	38,167
P	Monchique	-8,552	37,328
P	Paredes de Coura	-8,537	41,947
P	Feira	-8,535	40,928
P	Portimao	-8,522	37,130
P	Comdre o Coruche	-8,517	38,955
P	Gondomar	-8,517	41,140
P	Vila Nova de Famalicao	-8,512	41,452
P	Alcácer do Sal	-8,500	38,368
P	Condeixa-a-Nova	-8,500	40,103
P	Golega	-8,493	39,398
P	Oliveira de Baioro	-8,493	40,508
P	S. Joao de Madeira	-8,487	40,890
P	Albergaria-a-Velha	-8,485	40,697
P	Oliveira de Azemeis	-8,475	40,845
P	Moncao	-8,475	42,075
P	Santo Tirso	-8,470	41,345
P	Mealhada	-8,458	40,368
P	Lagoa	-8,453	37,130
P	Silves	-8,453	37,183
P	Agueda	-8,452	40,572
P	Vendas Novas	-8,447	38,667
P	Vilanova de Barquinha	-8,438	39,455
P	Anadia	-8,433	40,447
P	Braga	-8,433	41,557
P	Coimbra	-8,417	40,200
P	Coimbra	-8,417	40,213
P	Arcos de Valderez	-8,417	41,883
P	Ponte da Barca	-8,408	41,833
P	Tomar	-8,403	39,587

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	Penela	-8,403	40,022
P	Vilaverde	-8,373	41,670
P	Pacos de Ferreira	-8,357	41,280
P	Miranda do Corvo	-8,333	40,095
P	Constancia	-8,330	39,477
P	Guimaraes	-8,300	41,467
P	Ferreira do Zezere	-8,290	39,702
P	Penafiel	-8,282	41,202
P	Amares	-8,282	41,630
P	Castelo de Paiva	-8,278	41,043
P	Penacova	-8,277	40,272
P	Louzada	-8,273	41,272
P	Povoa de Lanhoso	-8,265	41,508
P	Albufeira	-8,260	37,083
P	Figueiro dos Vinhos	-8,255	39,890
P	Louza	-8,237	40,113
P	Mortágua	-8,225	40,403
P	Arouca	-8,225	40,928
P	Montemor	-8,215	38,630
P	Felgueiras	-8,195	41,368
P	Oliveira da Frades	-8,175	40,727
P	Mora	-8,157	38,942
P	Montemor-o-Novo	-8,155	38,633
P	Fafe	-8,150	41,455
P	Vieira	-8,138	41,652
P	Marco de Canavezes	-8,137	41,188
P	Loulé	-8,127	37,130
P	Santa Comba Bao	-8,120	40,350
P	Amorante	-8,072	41,290
P	Tondela	-8,070	40,517
P	S. Pedro do Sol	-8,058	40,758
P	Arganil	-8,047	40,218
P	Tálova	-8,037	40,358
P	Baiao	-8,023	41,153
P	Viana do Alentejo	-8,008	38,323
P	Celorico de Basto	-8,000	41,428
P	Arraiolos	-7,993	38,713
P	Carregal do Sal	-7,993	40,433
P	Faro	-7,942	37,017
P	CastroD'aire	-7,928	40,898
P	Evora	-7,907	38,560
P	Viseu	-7,903	40,657
P	Evora	-7,900	38,567
P	Cuba	-7,895	38,157
P	Beja	-7,872	38,008
P	Olhao	-7,860	37,025
P	Nelas	-7,850	40,535
P	Vidigueira	-7,802	38,202
P	Mangualde	-7,747	40,605
P	Tavira	-7,657	37,122
P	S. Fiel,	-7,500	40,033
P	Maura o Moura	-7,453	38,130
P	Vila Real do Santo António	-7,412	37,183
P	Guarda-Serra de Estrela	-7,110	40,535
P	illa Nova de Milfonte	-6,479	37,364
P	Lagos	-6,440	37,024
South Africa			
P	Springbok	17,883	-29,667
P	Hout Bay	18,350	-34,033
P	Western Cape, Table Mt.	18,417	-33,967
P	Western Cape, Capetown	18,417	-33,917
P	Cape Point	18,483	-34,350
P	Newlands	18,483	-33,967
P	Kogelberg Forest Reserve	18,567	-34,233
P	Jonkershoek	18,570	-33,580
P	Malmesbury	18,733	-33,450

Pres Lh	City/ Town/ Place	Longitude	Latitude
P	Somerset West	18,850	-34,083
P	Jonkershoek Mts., Stellenbosch	18,850	-33,933
P	Stellenboschberg	18,900	-33,967
P	Clanwilliam	18,900	-32,183
P	Betty's Bay	18,933	-34,367
P	Paarl	18,967	-33,733
P	Jonkershoek	18,967	-33,967
P	Porterville	18,983	-33,017
P	Wellington	19,000	-33,633
P	Kleinmond	19,033	-34,350
P	Ceres	19,317	-33,367
P	Robertson	19,883	-33,800
P	Bredasdorp	20,033	-34,533
P	Swellendam	22,433	-34,033
P	Western Cape, nr. George	22,450	-33,967
P	Graaff Reinet	24,550	-32,250
P	Northern Cape, Colesberg	25,100	-30,733
P	Port Elizabeth	25,583	-33,967
P	Eastern Cape, Somerset East	25,583	-32,717
P	Bloemfontein	26,200	-29,133
P	Eastern Cape, Queenstown	26,883	-31,900
P	East London	27,917	-33,033
P	Johannesburg	28,083	-26,200
P	Pretoria	28,217	-25,700
P	Mpumalanga, Nelspruit	30,967	-25,467
Spain			
P	Canarias, Orotava	-17,750	28,767
P	Canarias, Tenerife	-16,567	28,317
P	Canarias, Tenerife, Agua Mansa	-16,483	28,350
P	Canarias, Tenerife, Ladera de Guimar	-16,433	28,283
P	Canarias, Tenerife, Volcán de Guimar	-16,383	29,317
P	Canarias, Cruz de Tejeda	-15,600	28,017
P	Canarias, Santa Brígida	-15,500	28,033
P	Canarials, Gran Canaria, Las Palmas, Tafira Alta	-15,450	28,050
P	Canarias, Gran Canaria, Las Palmas, Teide	-15,417	28,000
P	Canarias, Las Palmas	-15,417	28,100
P	Galicia, La Coruña	-8,881	43,314
P	Galicia, Bayona, Mte. Ferro	-8,850	42,117
P	Galicia, Sanxenxo	-8,820	42,399
P	Galicia, Sangenjo-Pontevedra	-8,785	42,403
P	Galicia, Bayona	-8,660	42,120
P	Extremadura, Badajoz	-6,953	38,872
P	Andalucía, Doñana	-6,500	37,017
P	Andalucía, Villafranca Guadalquivir	-6,162	37,133
P	Andalucía, Conil	-6,073	36,295
P	Andalucía, Sevilla	-6,073	37,046
P	Andalucía, Doñana	-5,989	37,378
P	Andalucía, Punta de Tarifa-Cádiz	-5,608	36,017
P	Andalucía, Jimena de la Frontera-Cádiz	-5,465	36,420
P	Andalucía, Sotogrande	-5,358	36,256
P	Andalucía, Malaga	-4,417	36,717
P	Andalucía, Rincón de la Victoria	-4,281	36,714
P	Cantabria, Saja-Santander	-4,068	43,375
P	Madrid, Alarcón	-3,814	40,436
P	Andalucía, Punta de la Mona	-3,713	36,727
P	Madrid, Madrid	-3,698	40,412
P	Madrid	-3,683	40,400
P	Cantabria, Santander	-3,637	43,468
P	Andalucía, Punta de Jesús	-3,600	36,740
P	Andalucía, Cultivos de Salobreña	-3,567	36,740
P	Madrid, Aranjuez	-3,548	40,013
P	Andalucía, Puerto de Motril	-3,505	36,723
P	Andalucía, Motril	-3,500	36,740
P	Andalucía, Cultivos de Motril	-3,490	36,732
P	Andalucía, Torrenueva	-3,482	36,617
P	Andalucía, Desvío de Alpujarras	-3,482	36,860

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	Andalucía, Torrenueva	-3,477	36,713
P	Andalucía, Lanjarón	-3,467	36,927
P	Andalucía, Carchuna	-3,437	36,705
P	Andalucía, Castell de Ferro	-3,177	36,732
P	Andalucía, El Castillo de Huarca	-3,132	36,753
P	Catalunya, Platja d’Aro	-3,067	41,817
P	Castilla y León, Soria	-2,437	41,763
P	Murcia, La Alberca	-1,135	37,933
P	Murcia, Murcia	-1,132	37,982
P	Murcia, Cartagena	-1,040	37,629
P	València, Alberic	-1,035	39,782
P	Murcia, Torrevieja	-0,688	37,972
P	València, Guardamar	-0,651	38,147
P	València, Benimodo	-0,527	39,213
P	València, Sollana	-0,387	39,280
P	València, València	-0,376	39,482
P	València, El Saler	-0,323	39,388
P	València, Gola del Puchol-El Saler	-0,297	39,308
P	València, Ribesalbes	-0,280	40,021
P	València, Sagunto	-0,272	39,682
P	València, Benidorm	-0,125	38,536
P	València, Calpe	0,045	38,643
P	València, Oropesa-Castelló	0,110	40,092
P	València, Calpe	0,111	38,727
P	Catalunya, la Sénia	0,283	40,636
P	València, Oropesa	0,361	40,290
P	Catalunya, Ulldecona	0,448	40,598
P	Catalunya, Alcanar	0,482	40,545
P	Catalunya, Tortosa	0,523	40,812
P	Catalunya, Amposta	0,581	40,710
P	Catalunya, Sant Carles de la Ràpita	0,592	40,621
P	Catalunya, Rasquera	0,600	41,003
P	Catalunya, Ampolla	0,710	40,813

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	Catalunya, Deltebre	0,723	40,721
P	Catalunya, Ametlla de Mar	0,804	40,886
P	Catalunya, Hospitalet de l'Infant	0,925	40,992
P	Catalunya, Riudecols	0,977	41,170
P	Catalunya, Montbrió del Camp	1,005	41,121
P	Catalunya, Cambrils	1,054	41,075
P	Catalunya, Reus	1,109	41,156
P	Catalunya, Salou	1,134	41,077
P	Catalunya, Vila-seca	1,147	41,111
P	Catalunya, Tarragona	1,252	41,117
P	Catalunya, Altafulla	1,377	41,143
P	Catalunya, Torredembarra	1,400	41,146
P	Balears, Eivissa	1,433	38,910
P	Balears, Formentera, Estany Pudent	1,443	38,733
P	Balears, Jesús	1,460	38,933
P	Catalunya, Bisbal del Penedès	1,489	41,282
P	Catalunya, Coma-ruga	1,525	41,184
P	Catalunya, Vendrell	1,536	41,223
P	Catalunya, Calafell	1,570	41,202
P	Catalunya, Sant Martí Sarroca	1,612	41,386
P	Catalunya, Cunit	1,636	41,199
P	Catalunya, Vilafranca del Penedès	1,701	41,347
P	Catalunya, Canyelles	1,723	41,287
P	Catalunya, Vilanova i la Geltrú	1,726	41,224
P	Catalunya, Sant Pere de Ribes	1,774	41,263
P	Catalunya, Sant Sadurní d'Anoia	1,788	41,425
P	Catalunya, Sitges	1,812	41,238
P	Catalunya, Castelldefels	1,977	41,279
P	Catalunya, Terrassa	2,015	41,566
P	Catalunya, Rubí	2,033	41,493
P	Catalunya, Sant Cugat del Vallès	2,083	41,473
P	Catalunya, Prat de Llobregat	2,096	41,330
P	Catalunya, Barberà del Vallès	2,125	41,516

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	Catalunya, Barcelona	2,172	41,401
P	Catalunya, Montcada i Reixac	2,188	41,486
P	Catalunya, Aiguafreda	2,254	41,768
P	Catalunya, Seva	2,285	41,840
P	Catalunya, Granollers	2,291	41,608
P	Catalunya, Teia	2,324	41,498
P	Catalunya, Premià de Mar	2,360	41,491
P	Catalunya, Vilassar de Mar	2,393	41,505
P	Catalunya, Llinars del Vallès	2,402	41,640
P	Catalunya, Mataró	2,445	41,541
P	Balears, Capdellà	2,475	39,578
P	Catalunya, Sant Andreu de Llavaneres	2,483	41,573
P	Catalunya, Olot	2,489	42,183
P	Catalunya, Sant Celoni	2,492	41,689
P	Balears, Santa Ponsa	2,493	39,517
P	Balears, Sa Porrassa	2,500	39,500
P	Balears, Banyalbufar	2,512	39,690
P	Balears, Cala Vinyas-La Porrassa	2,528	39,508
P	Balears, Puigpunyent	2,528	39,625
P	Catalunya, Caldes d'Estrac	2,529	41,571
P	Balears, Esporlas	2,558	39,670
P	Balears, Son Vida	2,592	39,595
P	Balears, Génova-Son Dureta	2,597	39,558
P	Catalunya, Sant Pol de Mar	2,624	41,603
P	Catalunya, Hostalric	2,636	41,747
P	Catalunya, Anglès	2,639	41,958
P	Balears, Palma	2,657	39,578
P	Balears, Son Sardina	2,660	39,620
P	Catalunya, Calella	2,664	41,616
P	Catalunya, Santa Coloma de Farners	2,664	41,864
P	Catalunya, Pineda de Mar	2,691	41,627
P	Catalunya, Santa Susanna	2,708	41,636
P	Balears, Port de Sóller	2,708	39,795

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	Catalunya, Tordera	2,720	41,700
P	Catalunya, Malgrat de Mar	2,743	41,645
P	Catalunya, Sils	2,745	41,809
P	Balears, Mallorca, Bahía Azul	2,750	39,453
P	Balears, Arenal	2,750	39,500
P	Catalunya, Banyoles	2,767	42,119
P	Catalunya, Salt	2,788	41,975
P	Catalunya, Sant Llorenç de la Muga	2,791	42,321
P	Catalunya, Blanes	2,792	41,676
P	Balears, Alaró	2,792	39,707
P	Catalunya, Riudellots de la Selva	2,807	41,895
P	Catalunya, Caldes de Malavella	2,811	41,839
P	Catalunya, Fornells de la Selva	2,813	41,935
P	Catalunya, Girona	2,821	41,984
P	Catalunya, Quart	2,842	41,939
P	Mallorca, Cala Pi	2,842	39,363
P	Catalunya, Lloret de Mar	2,850	41,702
P	Catalunya, Cassà de la Selva	2,877	41,888
P	Catalunya, Llagostera	2,893	41,828
P	Balears, Mallorca, Lluchmajor	2,895	39,489
P	Catalunya, Bordils	2,913	42,045
P	Balears, Inca-Inca	2,913	39,718
P	Catalunya, Viladesens	2,932	42,096
P	Catalunya, Tossa de Mar	2,932	41,720
P	Balears, Mallorca, Sa Ràpita	2,938	39,367
P	Balears, Cabrera	2,943	39,133
P	Catalunya, Figueres	2,962	42,267
P	Balears, Inca-Sta. Magdalena	2,963	39,732
P	Catalunya, Sant Sadurni de l'Heura	2,993	41,958
P	Balears, Mallorca, Colònia St. Jordi	3,000	39,318
P	Catalunya, Santa Cristina d'Aro	3,001	41,814
P	Catalunya, Rupià	3,012	42,022
P	Catalunya, Corçà	3,018	41,989

Pres Lh	City/ Town/ Place	Longitude	Latitude
P	Catalunya, Sant Feliu de Guíxols	3,030	41,784
P	Catalunya, Castell d'Aro	3,030	41,817
P	Catalunya, Parlavà	3,032	42,024
P	Catalunya, Ultramort	3,036	42,038
P	Catalunya, Bisbal d'Empordà	3,040	41,959
P	Catalunya, Verges	3,048	42,063
P	Balears, Albufereta Pollensa	3,062	39,897
P	Catalunya, Platja d'Aro	3,068	41,819
P	Catalunya, Ullastret	3,070	42,001
P	Catalunya, Castelló d'Empúries	3,075	42,261
P	Catalunya, Viladamat	3,076	42,135
P	Catalunya, Calonge	3,077	41,862
P	Catalunya, Sant Pere Pescador	3,083	42,189
P	Catalunya, Bellcaire d'Empordà	3,096	42,080
P	Catalunya, Fontanilles	3,108	42,011
P	Catalunya, Ullà	3,109	42,052
P	Catalunya, Palau-sator	3,111	41,990
P	Balears, S'Albufera d'Alcúdia	3,115	39,795
P	Catalunya, Sant Martí d'Empúries	3,119	42,142
P	Catalunya, Torroella de Montgrí	3,129	42,043
P	Balears, Mallorca, Santanyí	3,130	39,356
P	Catalunya, Palamós	3,131	41,850
P	Catalunya, Llofriu	3,132	41,930
P	Catalunya, Escala	3,135	42,126
P	Catalunya, Pals	3,150	41,971
P	Catalunya, Palau-saverdera	3,151	42,310
P	Catalunya, Llançà	3,152	42,366
P	Catalunya, Palafrugell	3,165	41,918
P	Catalunya, Regencós	3,171	41,954
P	Catalunya, Cala Montgí	3,172	42,110
P	Catalunya, Roses	3,179	42,263
P	Catalunya, Calella de Palafrugell	3,186	41,890
P	Catalunya, Estartit	3,197	42,053
P	Catalunya, Tamariu	3,208	41,919
P	Catalunya, Begur	3,209	41,955
P	Catalunya, Cap de la Barra	3,213	42,057
P	Balears, Cap de Formentor	3,214	39,963
P	Catalunya, Fornells	3,216	41,940
P	Catalunya, Cadaqués	3,277	42,290
P	Balears, Mallorca, Coves del Drac	3,332	39,534
P	Balears, Mallorca, Coves d'Artà	3,455	39,658
P	Balears, Cala Gat-Capdepera	3,467	39,715
P	Balears, Cala Guyà	3,467	39,720
P	Balears, Minorca, Cala Forcat	3,833	40,000
P	Balears, Ciutadella	3,845	40,000
P	Balears, Galdana	3,997	39,935
P	Balears, Na Vermella	4,140	40,025
P	Balears, B. San Juan	4,220	39,915
P	Balears, Maó	4,250	39,943
P	Balears, Sant Felip	4,288	39,915
P	Balears, Alcaufar	4,292	39,832
P	Balears, Binisermanya	4,300	39,918
United Arab Emerates			
P	Al Ain	55,700	24,217
United Kingdom			
P	Glasgow	-4,250	55,833
P	Plymouth	-4,117	50,400
P	Exeter	-3,533	50,700
P	Edinburgh, Edinburgh	-3,250	55,933
P	Channel Islands, Guernsey	-2,467	49,483
P	Manchester, Fallowfield	-2,217	53,433
P	Cheshire, Broadbottom	-2,000	53,450
P	Chillingham	-1,900	55,517
P	Hertfordshire, Tring	-0,650	51,783
P	Farham House Lab, Imperial Bureau of Entomology	-0,617	51,533
P	Enfield	-0,067	51,667

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	Sussex, Lewes	-0,017	50,867
P	Eastbourne, East Sussex	0,250	50,800
P	W. Maidstone, Kent	0,517	51,267
P	Belfast, Windsor Park	-5,933	54,583
P	Edinburgh, Botanic Gardens	-3,200	55,950
Uruguay			
P*	Colonia, Carmelo	-58,283	-33,983
P*	Mercedes	-58,019	-33,256
P*	Colonia, Colonia del Sacramento	-57,841	-34,479
P*	Montevideo	-56,167	-34,850
P*	Carrasco	-56,061	-34,885
USA			
P	Hawaii, Kauai, Hanapepe town	-159,595	21,912
P	Hawaii, Kauai, Alakai Swamp	-159,558	22,108
P	Hawaii, Kauai, Poipu	-159,454	21,876
P	Hawaii, Kauai, Kokee	-159,392	22,075
P	Hawaii, Oahu, Hale'iwa	-158,113	21,590
P	Hawaii, Oahu, Opaeula	-158,055	21,351
P	Hawaii, Oahu, Ewa	-158,040	21,343
P	Hawaii, Oahu, Wahiawa	-158,024	21,503
P	Hawaii, Oahu, Waipahu	-158,003	21,231
P	Hawaii, Oahu, Pearl Harbor	-157,972	21,355
P	Hawaii, Oahu, Halawa	-157,912	21,383
P	Hawaii, Oahu, Honalulu	-157,858	21,307
P	Hawaii, Oahu, Mt. Tantalus	-157,818	21,336
P	Hawaii, Oahu, Kaneohe Bay	-157,810	21,463
P	Hawaii, Oahu, Kaneohe	-157,804	21,418
P	Hawaii, Oahu, Nr. Waimanalo	-157,721	21,350
P	Hawaii, Moanalua golf course	-157,536	21,221
P	Hawaii, Oahu, Fort Shafter	-157,531	21,212
P	Hawaii, Oahu, Nuuanu Valley	-157,501	21,203
P	Hawaii, Lanai, Lanai City	-156,922	20,831
P	Hawaii, Maui, Pukalani	-156,337	20,837
P	Hawaii, Maui, Auwahi	-156,333	20,638
P	Hawaii, Maui, Iao Needle	-156,332	20,532
P	Hawaii, Makawao	-156,313	20,857
P	Hawaii, Kalepeamoa	-156,285	20,701
P	Hawaii, Maui, Silversword Inn	-156,248	20,771
P	Hawaii, Maui, Haleakala National Park	-156,246	20,760
P	Hawaii, Maui, Hosmer Grove	-156,240	20,771
P	Hawaii, Maui, Olinda	-156,164	20,481
P	Hawaii, Hawaii, Pohakuloa	-155,650	18,934
P	Hawaii, Hawaii, Ahumoa	-155,614	19,812
P	Hawaii, Kemole	-155,528	19,880
P	Hawaii, Saddle Road, Kipuka Puuhuuhulu	-155,464	19,687
P	Hawaii, Kamuela	-155,421	20,015
P	Hawaii, Hawaii, Kipuka Puaulu	-155,304	19,447
P	Hawaii, Volcanos National Park, jagger museum	-155,290	19,422
P	Hawaii, Mauna Kea Volcano	-155,282	19,493
P	Hawaii, Volcanos National Park, visitor's center	-155,258	19,430
P	Hawaii, Kilauea crater	-155,250	19,417
P	Hawaii, Hawaii, Volcano	-155,238	19,431
P	Hawaii, Hawaii, Keauohana Forest Reserve	-154,954	19,420
P	Hawaii, Maui, Kula	-154,834	19,519
P	California, Humboldt, Eureka	-124,163	40,802
P	California, Humboldt, Redway	-123,817	40,117
P	Oregon, Josephine, Wonder	-123,534	42,364
P	California, Mendocino, Ukiah	-123,207	39,150
P	California, Sonoma, Russian R., 6km E Healdsburg	-122,800	38,600
P	California, Sonoma, Santa Rosa	-122,713	38,441
P	California, Sonoma, Petaluma	-122,636	38,233
P	California, Marin, Sausalito	-122,484	37,859
P	California, San Mateo, San Bruno Mt.	-122,433	37,683
P	California, Colusa, Leesville	-122,423	39,189
P	California, San Francisco	-122,418	37,775
P	California, Shasta, Redding	-122,391	40,587

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	California, San Francisco, Lake Merced	-122,294	37,432
P	California, Napa, Napa	-122,284	38,297
P	California, Alameda, Berkeley	-122,272	37,872
P	California, Alameda, Oakland	-122,270	37,804
P	California, Alameda, Berkeley	-122,250	37,867
P	California, Alameda	-122,241	37,765
P	California, Redwood City	-122,235	37,485
P	California, Alameda, Piedmont	-122,231	37,824
P	California, San Mateo, Jasper Ridge Biological Preserve	-122,226	37,408
P	California, Jasper Ridge Biological Preserve	-122,217	37,400
P	California, Glenn, Willows	-122,193	39,524
P	California, Contra Costa, Orinda	-122,179	37,877
P	California, Santa Clara, Palo Alto	-122,169	37,430
P	California, Contra Costa, Moraga	-122,129	37,835
P	California, Tehama	-122,122	40,027
P	California, Alameda, Melrose	-122,122	37,461
P	California, Yolo, 6km W Capay.	-122,117	38,700
P	California, Cache Creek	-122,060	38,710
P	California, Cupertino	-122,031	37,323
P	California, Santa Cruz, Santa Cruz	-122,030	36,974
P	California, Ulatis Creek	-121,990	38,360
P	California, Alameda, Fremont	-121,988	37,548
P	California, Solano, Vacaville	-121,987	38,357
P	California, San Ramon, Athens Downs Park	-121,977	37,780
P	California, Los Gatos	-121,974	37,227
P	California, Santa Clara, Santa Clara	-121,954	37,354
P	California, Campbell	-121,949	37,287
P	California, Santa Clara, San Jose	-121,894	37,339
P	California, Monterey, Monterey	-121,894	36,600
P	California, Santa Clara,	-121,878	37,199
P	California, Pleasanton	-121,874	37,663
P	California, Yolo, Woodland, Willow Slough	-121,785	38,605
P	California, Monterrey Big Sur	-121,783	36,267
P	California, Livermore	-121,767	37,682
P	California, Watsonville	-121,756	36,910
P	California, Yolo, Davis	-121,755	38,543
P	California, 0.6km S Arroyo Del Valle Sanatorium	-121,753	37,612
P	California, Willow Slough	-121,750	38,600
P	California, Yolo, Davis	-121,733	38,550
P	California, Monterey, Carmel	-121,731	36,480
P	California, Santa Clara, South Coyote	-121,717	37,200
P	California, Yolo, Grasslands Regional Park, 8km SE Davis.	-121,683	38,500
P	California, Monterey, Salinas	-121,654	36,678
P	California, Contra Costa, Byron Hot Springs	-121,632	37,847
P	California, Gilroy	-121,567	37,006
P	California, Santa Clara, Guadaloupe resvr.	-121,524	37,116
P	California, Sacramento, Sacramento	-121,493	38,582
P	California, Corral Hollow Creek	-121,460	37,660
P	California, Davis, University of California Davis	-121,445	38,323
P	California, San Joaquin, Stockton	-121,290	37,958
P	California, San Joaquin, Caswell State Park.	-121,183	37,700
P	California, Monterey, King City	-121,125	36,213
P	California, Lassen, Westwood Hills	-121,005	40,306
P	California, San Luis Obispo, Morro Bay State Park	-120,850	35,338
P	California, El Dorado, El Dorado	-120,847	38,683
P	California, Amador, Jackson	-120,773	38,349
P	California, San Luis Obispo, Oso Flaco Lake	-120,617	35,033
P	California, Modoc, Alturas	-120,541	41,487
P	California, Santa Barabara, Santa Maria	-120,435	34,953
P	California, Nevada, Truckee	-120,182	39,328
P	California, Santa Barbara, University of California Santa Barbara	-119,848	34,416
P	Nevada, Washoe, Reno	-119,813	39,530
P	California, Fresno, Fresno	-119,771	36,748
P	California, Santa Barabara, Santa Barabara	-119,697	34,421
P	California, Contra Costa, Fruitville	-119,082	35,383
P	California, Santa Paula	-119,058	34,354

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	California, Kern, Bakersfield	-119,018	35,373
P	California, Los Angeles, Santa Monica Mts.	-118,750	34,083
P	California, Los Angeles, Tapia Park	-118,706	34,085
P	California, Los Angeles, Westwood Park	-118,462	34,053
P	California, Los Angeles, El Segundo	-118,416	33,919
P	California, Santa Catalina, Avalon	-118,327	33,343
P	California, Los Angeles, Pacific Palisades	-118,313	34,025
P	California, Harbor City	-118,297	33,790
P	California, Los Angeles, University of California Los Angeles	-118,262	34,042
P	California, Los Angeles, Glendale	-118,254	34,143
P	California, Los Angeles, Los Angeles	-118,243	34,052
P	California, Los Angeles, Eagle Rock	-118,213	34,139
P	California, Los Angeles, University of Southern California	-118,171	34,012
P	California, Los Angeles, Pasadena	-118,144	34,148
P	California, Los Angeles, Altadena	-118,130	34,190
P	California, Los Angeles, Eagle Rock	-118,110	34,080
P	California, Los Angeles, San Gabriel	-118,105	34,096
P	California, Humboldt, Arcadia	-118,034	34,140
P	California, Los Angeles, Monrovia	-117,998	34,148
P	California, Orange, Newport Beach	-117,928	33,619
P	California, Orange, Fullerton	-117,924	33,870
P	California, Orange, Costa Mesa	-117,918	33,641
P	California, Los Angeles, Azusa	-117,907	34,134
P	California, Orange, Santa Ana	-117,867	33,746
P	California, Los Angeles, Tanbark Flats	-117,760	34,204
P	California, Los Angeles, Pomona	-117,751	34,055
P	California, Orange, San Juan Canyon	-117,706	33,508
P	California, San Bernadino, Ontario	-117,650	34,063
P	California, San Bernadino, Upland	-117,648	34,098
P	California, Alta Loma	-117,597	34,122
P	California, Rancho Cucamonga	-117,592	34,106
P	California, Orange, Trabuco Canyon	-117,577	33,657
P	Washington, Spokane, Spokane	-117,425	47,659

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	California, San Diego, Point Loma	-117,400	33,217
P	California, Riverside, Riverside	-117,395	33,953
P	California, San Diego, San Luis Rey River	-117,391	33,202
P	California, San Diego, San Diego	-117,350	33,367
P	California, San Diego, Mission Hills	-117,317	33,250
P	California, Grand Terrace	-117,313	34,034
P	California, San Bernadino, San Bernadino	-117,289	34,108
P	California, Riverside, Temecula	-117,288	33,505
P	California, San Diego, La Jolla	-117,273	32,847
P	California, San Diego, Encinitas, Oak Crest Park	-117,267	33,033
P	California, San Diego, 1mi S Del Mar	-117,264	32,945
P	California, San Diego, Del Mar	-117,264	32,959
P	California, San Diego, Encinitas	-117,260	33,050
P	California, San Diego, Torrey Pines State Reserve	-117,252	32,915
P	California, San Diego, Point Loma	-117,251	32,723
P	California, San Diego, Torrey Pines State Res.	-117,250	32,917
P	California, San Diego, Del Mar, Torrey Pines St. Park	-117,247	32,941
P	California, San Diego, La Jolla	-117,240	32,850
P	California, San Diego, Balboa Park	-117,233	33,217
P	California, San Diego, Del Mar, Carmel Mountain	-117,217	33,931
P	California, San Diego, San Diego	-117,212	32,815
P	California, San Diego, Rancho Santa Fe	-117,202	33,020
P	California, San Diego, San Clemente Creek	-117,200	32,833
P	California, San Diego, San Diego	-117,200	33,200
P	California, University of California Riverside	-117,195	33,582
P	California, San Diego, San Diego	-117,166	32,737
P	California, San Diego, pacific beach	-117,150	33,233
P	California, San Diego, Balboa Park	-117,146	32,732
P	California, San Diego, Kate Sessions Park	-117,133	33,283
P	California, San Diego, Imperial Beach, Tiajuana River Estuary	-117,117	32,550
P	California, San Diego, University of California Elliot Chaparral Reserve	-117,108	32,892
P	California, San Diego, University of California Elliot Chaparral Reserve	-117,100	32,900
P	California, Riverside, Temecula	-117,100	33,465

Pres Lh	City/ Town/ Place	Longitude	Latitude
P	California, San Diego, Escondido	-117,086	33,119
P	California, San Diego, San Diego	-117,057	32,748
P	California, San Diego, Chula Vista	-117,037	32,642
P	California, Riverside, Lake Skinner Camp C	-117,033	33,583
P	California, Riverside, Temecula, Lake Skinner County Park	-117,031	33,352
P	California, San Diego, Chula Vista	-117,026	32,644
P	California, San Diego	-117,003	32,413
P	California, San Diego, Chula Vista	-116,993	32,651
P	California, San Diego, El Cajon	-116,980	32,790
P	California, San Diego, Sweet Water Wildlife Refuge	-116,952	32,721
P	California, San Diego, El Cajon	-116,946	32,810
P	California, Riverside, Palm Springs	-116,544	33,830
P	Nevada, Clark, Las Vegas	-115,136	36,175
P	Arizona, Yuma, Yuma	-114,624	32,725
P	Arizona, Maricopa, Phoenix	-112,073	33,448
P	Arizona, Pima, Tucson	-110,553	32,132
P	Arizona, Cochise, Douglas	-109,545	31,344
P	Texas, Lubbock , Lubbock	-101,855	33,578
P	Texas, Bexar, San Antonio, Brackenridge Park	-98,493	29,424
P	Texas, Bexar, Brackenridge Park	-98,473	29,456
P	Texas, Brownsville	-97,497	25,901
P	Texas, Williamson, Taylor	-97,409	30,571
P	Texas, Dallas, Dallas	-96,800	32,783
P	South Dakota, Brookings, Brookings	-96,798	44,311
P	Oklahoma, Caddo	-96,263	34,127
P	Texas, Hopkins , Sulphur Springs	-95,601	33,138
P	Texas, Harris, Houston	-95,363	29,763
P	Texas, Jefferson, Beaumont	-94,102	30,086
P	Texas, Bowie, Texarkana	-94,048	33,425
P	Arkansas, Miller, Texarkana	-94,038	33,442
P	Louisiana, Caddo, Shreveport	-93,750	32,525
P	Louisiana, Calcasieu, Lake Charles	-93,217	30,226
P	Minnesota, Ramsey, St. Paul	-93,093	44,944

Pres Lh	City/ Town/ Place	Longitude	Latitude
P	Louisiana, Evangeline	-92,571	30,262
P	Louisiana, Rapides, Alexandria	-92,445	31,311
P	Louisiana, Rapides, Cheneyville	-92,287	31,015
P	Louisiana, St. Landry, Opelousas	-92,081	30,533
P	Louisiana, Avoyelles, Mansura	-92,049	31,058
P	Louisiana, Lafayette, Lafayette	-92,020	30,224
P	Louisiana, Iberia, New Iberia	-91,819	30,003
P	Louisiana, Franklin	-91,501	29,796
P	Louisiana, Pointe Coupee	-91,433	30,734
P	Mississippi, Wilkinson, Woodville	-91,299	31,104
P	Louisiana, St. Mary, Berwick	-91,219	29,694
P	Louisiana, St. Mary, Morgan City	-91,207	29,699
P	Louisiana, E. Baton Rouge, Baton Rouge	-91,154	30,451
P	Louisiana, Ascension, Donaldsonville	-90,993	30,101
P	Louisiana, Madison, Delta	-90,927	32,326
P	Mississippi, Warren, Vicksburg	-90,878	32,353
P	Louisiana, St. James, Convent	-90,830	30,021
P	Louisiana, Lafourche, Thibodeaux	-90,823	29,796
P	Louisiana, Terrebonne, Schriever	-90,810	29,742
P	Louisiana, Acadia	-90,801	29,769
P	Louisiana, St. Charles	-90,721	29,753
P	Louisiana, Houma	-90,719	29,596
P	Louisiana, Tangipahoa	-90,512	30,876
P	Mississippi, Copiah, Hazlehurst	-90,396	31,860
P	Mississippi, Copiah, Crystal Springs	-90,357	31,987
P	Missouri, St. Louis, University City	-90,309	38,656
P	Louisiana, New Orleans, Kenner	-90,259	33,039
P	Missouri, St. Louis, St. Louis, Botanic Gardens	-90,198	38,627
P	Mississippi, Hinds, Jackson area	-90,185	32,299
P	Louisiana, Jefferson	-90,153	29,966
P	Louisiana, Orleans, Audubon Park	-90,126	29,931
P	Louisiana, West End	-90,113	30,023
P	Louisiana, Orleans, New Orleans	-90,075	29,954

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	Louisiana, New Orleans	-90,067	29,967
P	Louisiana, Milneburg	-90,061	30,024
P	Tennessee, Shelby, Memphis	-90,049	35,149
P	Louisiana, Algiers	-90,047	29,945
P	Louisiana, St. Bernard	-89,859	29,867
P	Mississippi, Holmes, Durant	-89,854	33,075
P	Mississippi, Madison, Camden	-89,839	32,782
P	Louisiana, Plaquemines, Happy Jack	-89,734	29,522
P	Louisiana, Plaquemines, Happy Jack	-89,733	29,517
P	Louisiana, Nairn, Nairn	-89,611	29,428
P	Mississippi, Covington, Collins	-89,555	31,645
P	Mississippi, Holmes, Holmes County State Park	-89,546	33,014
P	Louisiana, Plaquemines, Buras	-89,524	29,352
P	Mississippi, Forrest, Hattiesburg	-89,290	31,327
P	Mississippi, Hancock, Bay Saint Louis	-89,195	30,183
P	Mississippi, Choctaw, Ackerman	-89,173	33,310
P	Mississippi, Perry	-89,141	30,721
P	Mississippi, Jones, Laurel	-89,131	31,694
P	Mississippi, Harrison, Gulfport	-89,093	30,367
P	Tennessee, Obion, Kenton	-89,012	36,202
P	Mississippi, Oktibbeha, 3mi W Adaton	-88,970	33,483
P	Mississippi, Harrison, Biloxi	-88,885	30,396
P	Mississippi, Jackson, Ocean Springs	-88,828	30,411
P	Mississippi, Oktibbeha, Starkville	-88,818	33,450
P	Mississippi, Oktibbeha, Starkville	-88,817	33,450
P	Mississippi, Lauderdale, Meridian	-88,704	32,364
P	Mississippi, Clay, West Point	-88,650	33,608
P	Mississippi, Jackson, Pascagoula	-88,556	30,366
P	Mississippi, Monroe, Aberdeen	-88,544	33,825
P	Mississippi, Lowndes, Columbus	-88,427	33,496
P	Mississippi, Clarke, Clarke County State Park	-88,415	32,055
P	Mississippi, Leflore, Greenwood Springs	-88,309	33,887
P	Alabama, Mobile, Mobile	-88,043	30,694
P	Illinois, Cook, Chicago	-87,650	41,850
P	Florida, Escambia, Gonzalez	-87,291	30,581
P	Florida, Escambia, Pensacola	-87,217	30,421
P	Tennessee, Giles, Pulaski	-87,031	35,200
P	Alabama, Jefferson, Birmingham	-86,803	33,521
P	Florida, Okaloosa, Crestview	-86,571	30,762
P	Tennessee, Lincoln, Fayetteville	-86,571	35,152
P	Florida, Okaloosa, Niceville	-86,482	30,517
P	Tennessee, Davidson, Nashiville	-86,470	36,096
P	Alabama, Auburn University	-85,485	32,602
P	Florida, Gulf, Port Saint Joe	-85,303	29,812
P	Georgia, Meriweather,Talbot, Manchester	-84,620	32,860
P	Georgia, Fulton, Atlanta	-84,388	33,749
P	Georgia, Gwinnett, Watton, Loganville	-83,540	33,502
P	South Carolina, Pickens, Clemson	-82,838	34,683
P	Florida, Pinellas, St. Petersburg	-82,679	27,771
P	Florida, Hillsborough, Tampa	-82,459	27,947
P	Florida, Hillsborough, Temple Terrace	-82,389	28,035
P	South Carolina, Greenville, Travelers Rest	-82,264	34,580
P	South Carolina, McCormick, McCormick	-82,174	33,545
P	South Carolina, Laurens, Gray Court	-82,114	34,608
P	Georgia, Richmond, Augusta	-81,975	33,471
P	Florida, Polk, Winter Haven	-81,733	28,022
P	Florida, Duval, Jacksonville	-81,656	30,332
P	Florida, Highlands, Sebring	-81,441	27,495
P	Florida, Orange, Orlando	-81,379	28,538
P	Florida, Seminole, Sanford	-81,273	28,800
P	South Carolina, York	-81,250	35,000
P	South Carolina, York, York	-81,242	34,994
P	Florida, Seminole, Oviedo	-81,208	28,670
P	North Carolina, Gaston, Belmont	-81,038	35,243
P	South Carolina, Orangeburg, Orangeburg	-80,856	33,492
P	Florida, Palm Beach, John Stretch Park	-80,815	26,693

Pres Lh	*City/ Town/ Place*	*Longitude*	*Latitude*
P	Florida, Broward, Davie	-80,233	26,063
P	North Carolina, Winston-Salem	-80,144	36,056
P	South Carolina, Dorchester, Sumerville	-80,103	33,011
P	Florida, Palm Beach, Delray Beach	-80,073	26,461
P	South Carolina, Charleston, Charleston	-79,931	32,776
P	South Carolina, Florence, Florence	-79,763	34,195
P	South Carolina, Georgetown, Georgetown	-79,295	33,377
P	South Carolina, Charleston, McClellanville	-79,274	33,052
P	North Carolina, Orange, Chapel Hill	-79,056	35,913
P	North Carolina, Wake, Raleigh	-78,639	35,772
P	North Carolina, Wayne, Goldsboro	-77,993	35,385
P	North Carolina, New Hanover, Wilmington	-77,945	34,226
P	Maryland, Baltimore, Baltimore	-76,613	39,290
Venezuela			
P	Aragua, Parque Nacional Rancho Grande	-67,686	10,349
Zimbabwe			
P	Kolwa	32,667	-17,050

Annexe 2 Sources of *Linepithema humile*'s occurrences

Museum collections:
Archbold Biological Station, Lake Placid, Florida, USA;
Bishop Museum, University of Hawaii, Honolulu, Hawaii, USA;
British Museum of Natural History, London, United Kingdom;
California Academy of Sciences, San Francisco, California, USA;
California State University, Northridge, California, USA;
Clemson University, Clemson, South Carolina, USA.
Combined Scientific Supplies, Midland, Texas, USA;
Department of Entomology, University of Minnesota, Minneapolis, Minnesota, USA;
Entomology Museum, Oregon Department of Agriculture, Salem, Oregon, USA;
Entomology Research Museum, University of California, Riverside, California, USA;
Essig Museum of Entomology, University of California, Berkeley, California, USA;
Field Museum, Chicago, Illinois, USA;
Florida Department of Agriculture and Consumer Services, Tallahassee, Florida, USA;
Hawaii Department of Agriculture, Honolulu, Hawaii, USA;
Honolulu Office, United States Geological Survey, Honolulu, Hawaii, USA;
Instituto Fundación Miguel Lillo, Tucumán, Argentina;
Los Angeles County Natural History Museum, Los Angeles, California, USA;
Michigan State University, Lansing, Michigan, USA;
Mississippi Entomological Museum, Mississippi State University, Mississippi, USA;
Museo Argentina de Ciencias Naturales, Buenos Aires, Argentina;
Museo Civico de Historia Natural 'Giacomo Doria', Genoa, Italy;
Museo de Zoología de la Pontificia, Universidad Católica del Ecuador, Quito, Ecuador;
Museo Nacional de la Historia Natural del Paraguay, San Lorenzo, Paraguay;
Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil;
Muséum d'Histoire Naturelle, Geneva, Switzerland;
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA;
Museum of Zoology, University of Michigan, Ann Arbor, Michigan, USA;
National Museum of Natural History, Smithsonian Institution, Washington DC, USA;
Natural History Museum of Los Angeles County, Los Angeles, California, USA;
Naturhistorisches Museum, Basel, Switzerland;
Naturhistorisches Museum Wien, Vienna, Austria;
Ohio State University, Columbus, USA;
Oklahoma State University, Stillwater, Oklahoma, USA;
Oregon Department of Agriculture, Salem, Oregon, USA;
Pennsylvania State University, Pennsylvania, USA;
Plant Industry Division, Plant Protection Section, North Carolina Department of Agriculture, Raleign, North Carolina, USA;
R. M. Bohart Museum of Entomology, Davis, California, USA;
Snow Entomological Collections, Natural History Museum, University of Kansas, Lawrence, Kansas, USA;

South Dakota State University, Brookings, South Dakota, USA;
Texas A&M University Insect Collection, College Station, Texas, USA;
University of Arizona, Tuscon, Arizona, USA;
University of Arkansas, Fayetteville, Arkansas, USA;
University of Colorado, Boulder, Colorado, USA;
University of Delaware, Newark, Delaware, USA;
University of New Hampshire Insect Collection, Durham, New Hampshire, USA.

Personal collections:
Andrew V. Suarez personal collection, Urbana, Illinois, USA;
Alexander L. Wild personal collection, Davis, California, USA.
Crisanto Gómez personal collection, Girona, Catalunya, Spain;
Philip S. Ward personal collection, Davis, California, USA;
William P. MacKay personal collection, El Paso, Texas, USA;
Xavier Espadaler personal collection, Barcelona, Catalunya, Spain;
Yoshifumi Touyama personal collection, Higashi-Hiroshima, Japan;

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Annexe 3 Occurrence data of Argentine Ant (*Linepithem humile*) in Catalonia in UTM coordinates (and European 1950 Datum). The first column refers to presence (P) or absence (A) of the species. Symbol (*) indicates those occurrences data obtained during the field work, while the rest has been obtained from personal collections and scientific literature (Annexe 4).

Pres lh	*City/ Town/ Place*	*Longitude*	*Latitude*	*Date*
A*	Puigcerda	411850	4698600	22/05/03
A*	Sort	346225	4697350	21/06/03
A*	Bellver de Cerdanya	399325	4691875	23/06/03
A*	Martinet	392680	4690850	23/06/03
A*	Seu d'Urgell	373400	4690800	21/06/03
P	Llança	512550	4690500	
A	Molló	451075	4688750	?/?/03
P	Sant Llorenç de la Muga	482750	4685575	?/?/03
A	Camprodon	447800	4685025	26/06/03
A	Ribes de Freser	431700	4684475	26/06/03
P	Palau-saverdera	512425	4684250	
P	Cadaqués	522850	4682125	
A*	Pobla de Segur	332475	4679525	21/05/03
P	Figueres	496900	4679450	
P	Roses	514800	4679100	20/08/03
P	Castello d'Empúries	506175	4678800	
A*	Baga	406270	4678681	23/06/03
A	Ripoll	433350	4672350	?/07/03
P	Sant Pere Pescador	506850	4670850	?/?/03
A*	Tremp	326000	4670700	21/06/03
A*	Coll de Nargo	361025	4670650	21/06/03
P	Olot	457825	4670325	
A*	Bàscara	492650	4667800	26/06/03
A	Santa Pau	464650	4666075	?/?/03
P	Sant Marti d'Empúries	509820	4665590	
A*	Isona	338600	4664950	21/06/03
P*	Viladamat	506300	4664800	26/06/03
P	Escala	511150	4663875	
P	Banyoles	480700	4663050	
P	Cala Montgó	514260	4662060	
A*	Berga	404657	4661908	23/06/03
A	Albons	506700	4661850	02/07/03
P	Viladesens	494350	4660550	
A*	Vilafreser	490230	4659410	26/06/03
A*	Oliana	360550	4658950	21/06/03
P	Bellcaire d'Empordà	507950	4658750	?/?/03
A*	Sant Feliu de Pallerols	459375	4658500	28/06/03
P	Verges	503950	4656850	?/?/03
P	Cap de la Barra	517600	4656240	
P	Estartit	516320	4655750	
P	Ullà	509025	4655625	17/06/03
A	Torelló	439191	4655576	25/06/03
P	Bordils	492825	4654825	
P	Torroella de Montgrí	510650	4654650	?/?/03
P	Ultramort	502950	4654050	02/07/03
P	Canet d'Adri	478531	4653718	?/07/05
A	Gualta	508675	4653150	02/07/03
A	Serra de Daró	506100	4653050	17/06/03
P	Parlavà	502675	4652500	02/07/03
A	Pera	497950	4652300	17/06/03
P	Rupià	500975	4652250	17/06/03
A*	Amer	467200	4651225	28/06/03
P	Fontanilles	508950	4651100	17/06/03
A*	Solsona	377500	4650575	21/06/03
A	Manlleu	440663	4650218	25/06/03
P	Ullastret	505775	4650025	17/06/03
P	Palau-sator	509200	4648750	17/06/03
P	Corça	501500	4648650	17/06/03
P	Girona	485175	4648075	
A	Peratallada	507530	4647400	02/07/03
P	Salt	482450	4647150	
P	Pals	512425	4646650	
A	Vulpellac	504620	4645620	02/07/03
P	Bisbal d'Empordà	503350	4645350	
P*	Anglés	470075	4645250	28/06/03
P*	Sant Sadurní de l'Heura	499400	4645150	26/06/03
A*	Cruïlles	501150	4645120	26/06/03
P*	Begur	517300	4644925	26/06/03

Pres lh	City/ Town/ Place	Longitude	Latitude	Date
P*	Regencós	514200	4644725	26/06/03
A	Torrent d'Empordà	510600	4644525	02/07/03
P*	Fornells	517940	4643220	26/06/03
P	Quart	486900	4643150	
P*	Fornells de la Selva	484500	4642700	09/09/03
A	Vic	438306	4642404	28/06/03
P*	Llofriu	510980	4642140	26/06/03
A*	Sant Pol	503100	4642130	26/06/03
A*	Ponts	349650	4642100	22/05/03
A	Sant Julià de Vilatorta	444082	4641639	?/?/03
A*	Cardona	390750	4641250	21/06/03
P*	Tamariu	517240	4640920	26/06/03
P	Palafrugell	513700	4640800	
A*	Artesa de Segre	338150	4640200	22/05/03
A*	Navàs	407121	4639604	23/06/03
P*	Riudellots de la Selva	483950	4638200	09/09/03
P	Calella de Palafrugell	515460	4637670	?/?/03
P	Cassà de la Selva	489825	4637475	?/?/03
A*	Sant Maria d'Oló	420134	4636422	20/05/03
A	Taradell	440892	4636009	?/?/03
P*	Santa Coloma de Farners	472125	4634800	28/06/03
P	Calonge	506350	4634500	
A*	Tona	436018	4633478	10/06/03
A*	Viladrau	449450	4633250	10/06/03
P	Palamos	510900	4633250	
P	Seva	440658	4632318	
A*	Súria	396477	4632272	21/06/03
P*	Caldes de Malavella	484275	4631975	01/09/03
P	Llagostera	491150	4630800	?/?/03
P*	Riudarenes	476550	4630250	18/06/04
P	Platja d'Aro	505665	4629715	
A*	Arbúcies	459875	4629650	10/06/03
P	Castell d'Aro	502510	4629500	
P	Santa Cristina d'Aro	500100	4629200	
A*	Balaguer	317825	4629050	22/05/03
P	Sils	478800	4628650	?/?/03
P	Sant Feliu de Guíxols	502475	4625875	
A*	Massanes (train station)	472980	4624740	28/06/03
P*	Aiguafreda	438028	4624410	10/06/03
P	Castellterçol	427049	4622611	?/?/03
P*	Hostalric	469750	4621875	28/06/03
A*	Calaf	376408	4621358	20/05/03
P*	Lloret de Mar	484883	4621008	18/06/04
A*	Manresa	402462	4620400	20/05/03
A*	Breda i Riells-Viabrea	464197	4619719	10/06/03
P*	Lloret de Mar	485544	4619538	18/06/04
P*	Lloret de Mar	486311	4618900	18/06/04
P	Tossa de Mar	494350	4618750	
P	Lloret de Mar	487500	4616750	
P	Tordera	476693	4616603	
P*	Sant Celoni	457714	4615494	10/06/03
A*	Garriga	440705	4615035	10/06/03
A*	Cervera	356250	4614750	20/05/03
P*	Cala Sant Francesc (Blanes)	483937	4614271	18/06/04
P	Blanes	482650	4613925	
A*	Tàrrega	345250	4612600	20/05/03
A*	Mollerussa	324750	4611025	20/05/03
P*	Malgrat de Mar	478580	4610460	16/05/03
A*	Lleida	302200	4610300	20/05/03
P*	Llinars del Vallés	450207	4610046	10/06/03
P	Santa Susanna	475682	4609493	
P	Pineda de Mar	474260	4608445	
P*	Calella	472014	4607306	16/05/03
P	Granollers	440939	4606563	
P	Sant Pol de Mar	468695	4605801	?/?/03
A*	Igualada	384825	4604075	17/06/03
A*	Arenys de Mar	462519	4603449	16/05/03
P	Sant Andreu de Llavaneres	456871	4602548	?/?/03
P	Caldes d'Estrac	460711	4602364	?/?/03
P	Vacarisses	408280	4602331	?/?/03
P	Terrassa	417894	4602110	
A*	Santa Coloma de Queralt	365225	4599325	17/06/03

Pres Ih	City/ Town/ Place	Longitude	Latitude	Date
A*	Esparraguera	405802	4599324	17/06/03
P*	Mataro	453731	4599067	06/05/03
A*	Borges Blanques	322300	4598950	21/05/03
P	Barberà del Vallés	426944	4596449	
P	Vilassar de Mar	449323	4595034	
P	Teia	443587	4594332	
P	Rubi	419237	4593980	
P	Premià de Mar	446560	4593555	
P	Montcada i Reixac (Montcada)	432200	4593150	
A*	Llacuna	377616	4592444	17/06/03
P	Sant Cugat del Vallés	423467	4591732	
A*	Sant Pere de Riudebitlles	391801	4589791	16/06/03
P*	Sant Sadurní d'Anoia	398760	4586764	16/06/03
P	Barcelona	430743	4583711	
P*	Sant Martí Sarroca	383954	4582667	17/06/03
A*	Montblanc	346450	4582250	21/05/03
A*	Avinyonet del Penedés	397872	4579783	16/06/03
A	Lilla	350480	4579160	?/?/03
P*	Vilafranca del Penedés	391354	4578122	16/06/03
A*	Begues	409836	4576374	16/06/03
P	Prat de Llobregat	424372	4575838	29/08/03
A*	Olivella	400563	4574040	16/06/03
A*	Valls	353625	4572250	21/05/03
P*	Canyelles	393085	4571539	16/06/03
A*	Rodonya	365900	4571350	16/06/03
P*	Bisbal del Penedés	373450	4571200	16/06/03
P	Castelldefels	414300	4570300	
P*	Sant Pere de Ribes	397269	4568755	16/06/03
A*	Flix	294750	4567450	21/05/03
P*	Sitges	400439	4565891	16/06/03
P	Vendrell	377300	4564575	
P*	Vilanova i la Geltrú	393250	4564500	16/06/03
P	Calafell	380100	4562200	
P	Cunit	385625	4561850	
P	Coma-ruga	376280	4560260	
P*	Riudecols	330300	4559650	21/05/03
P*	Reus	341350	4557850	21/05/03
A*	Falset	317175	4557350	21/05/03
P*	Torredembarra	365700	4556225	11/06/03
P	Altafulla	363800	4555925	
P*	Montbrió del Camp	332500	4554225	12/06/03
P*	Tarragona	353250	4553350	11/06/03
P	Vila-seca	344400	4552850	?/?/03
A*	Mora la Nova	302725	4552550	21/05/03
P*	Salou	343250	4549100	11/06/03
P*	Cambrils	336550	4548950	12/06/03
A*	Gandesa	284850	4548050	12/06/03
A*	Vandellos	317725	4543400	12/06/03
P*	Rasquera	298150	4541975	12/06/03
P*	Hospitalet de l'Infant	325440	4540000	12/06/03
A*	Benifallet	291150	4539050	12/06/03
A*	Tivenys	290575	4531675	12/06/03
P*	Ametlla de Mar	314950	4528450	12/06/03
A*	Perelló	307300	4527600	12/06/03
P*	Tortosa	291100	4520925	12/06/03
P*	Ampolla	306850	4520650	12/06/03
P*	Deltebre	307700	4510350	12/06/03
P*	Amposta	295650	4509450	12/06/03
P*	Sènia	270200	4501975	12/06/03
P*	Sant Carles de la Ràpita	296350	4499500	12/06/03
P*	Ulldecona	284025	4497350	12/06/03
P*	Alcanar	286800	4491400	12/06/03

Annexe 4 Sources of *Linepithema humile*'s occurrences

Personal collections:
Crisanto Gómez personal collection, Girona, Catalunya, Spain.
Xavier Espadaler personal collection, Barcelona, Catalunya, Spain.

Scientific literature:

Arnan, X. 2004 *Influència dels patrons regionals i de vegetació en la recuperació post incendi de les comunitats de formigues mediterrànies*. DEA thesis. Bellaterra: Universitat Autònoma de Barcelona.
Collingwood, C. A. & Yarrow, I. H. H. 1969 A survey of Iberian Formicidae (Hymenoptera). *Eos* 44, 53-101.
Espadaler, X. & Gómez, C. 2003 The Argentine ant, *Linepithema humile*, in the Iberian Peninsula. *Sociobiology* 37, 3-25.
Giraud, T., Pedersen, J. S. & Keller, L. 2002 Evolution of supercolonies: The Argentine ant of southern Europe. *Proc. Nat. Acad. Sci. USA* 99, 6075-6079.
Suñer, D. 1991 Contribució al coneixement mirmecològic de Gavarres, Montgrí, Guilleries i la Serralada Transversal. Ph D Thesis. Bellaterra: Universitat Autònoma Barcelona.

Field work:
It was done with the valuable collaboration and assitance of J.M. Bas, Q. Gubau and S. Abril. In addition, X. Espadaler, C. Gómez, X. Blancafort, P. Pons, M.R. Hernández, J. Oliveras and M. Sàbat also provided Argentine ant occurrence data.

Annexe 5 Occurrence data of Argentine Ant (*Linepithem humile*) in the Costa Brava in UTM coordinates (and European 1950 Datum). The first column refers to presence (P) or absence (A) of the species collected during a field work sampling, with the assistance of A. Seglar, J.M. Bas, C. Roura, and X. Nogués.

Pres Lh	*Longitude*	*Latitude*	*Date*
A	482411.73	4614639.68	23/05/05
A	482212.39	4614724.12	23/05/05
A	481154.10	4614724.75	23/05/05
A	482257.20	4614798.24	23/05/05
A	482667.57	4614948.83	23/05/05
A	482643.56	4615143.55	23/05/05
A	480697.06	4615201.02	23/05/05
A	483483.03	4615491.67	23/05/05
A	483235.13	4615554.01	23/05/05
P	482384.59	4615581.44	23/05/05
P	480279.97	4615643.76	23/05/05
P	482288.37	4615730.74	23/05/05
A	480073.63	4615755.58	23/05/05
A	483255.72	4615823.92	23/05/05
P	484142.02	4615835.35	23/05/05
P	483406.72	4616165.87	23/05/05
P	484458.12	4616170.41	23/05/05
A	479432.06	4616237.94	23/05/05
P	484099.81	4616321.51	23/05/05
P	484354.28	4616340.51	23/05/05
P	484244.59	4616403.89	23/05/05
P	485062.58	4616421.49	23/05/05
A	479786.97	4616484.13	23/05/05
A	483389.98	4616496.37	23/05/05
P	484066.23	4616497.95	23/05/05
P	485552.48	4616565.18	23/05/05
P	485428.77	4616593.75	23/05/05
A	483131.86	4616662.20	23/05/05
P	485390.44	4616670.62	23/05/05
P	485346.71	4616763.96	23/05/05
A	480162.09	4616989.36	23/05/05
P	485755.00	4617094.00	29/04/05
A	480391.35	4617121.21	23/05/05
P	485730.00	4617162.00	29/04/05
A	480505.67	4617219.69	23/05/05
P	485660.00	4617259.00	29/04/05
A	480581.81	4617287.83	23/05/05
P	489785.41	4617305.02	30/05/05
P	485671.00	4617307.00	29/04/05
A	480523.61	4617408.48	23/05/05
P	489726.22	4617432.19	30/05/05
A	480830.69	4617457.50	23/05/05
P	480332.58	4617488.23	23/05/05
P	485466.00	4617509.00	29/04/05
P	489541.47	4617551.33	30/05/05
P	489772.54	4617643.79	30/05/05
A	480271.32	4617671.65	23/05/05
P	489831.73	4617790.67	?/07/04
A	490109.13	4617851.96	?/07/04
A	482678.00	4617971.00	29/04/05
P	491218.58	4618004.72	?/07/04
P	480239.92	4618115.65	23/05/05
P	490710.34	4618128.73	?/07/04
A	485569.00	4618143.00	29/04/05
P	489958.53	4618275.84	30/05/05
P	486185.00	4618321.00	29/04/05
P	480339.81	4618354.13	23/05/05
P	490035.59	4618365.57	30/05/05
P	490527.12	4618420.84	10/06/05
P	490505.19	4618423.38	10/06/05
P	490556.41	4618423.49	10/06/05
P	490492.66	4618432.61	10/06/05
P	490572.73	4618435.28	10/06/05
P	490492.83	4618437.92	10/06/05
P	490017.51	4618438.07	?/07/04
P	490456.54	4618439.03	10/06/05
P	490497.29	4618457.07	10/06/05
P	490515.61	4618459.45	10/06/05
P	490528.48	4618463.75	10/06/05
P	490442.02	4618464.83	10/06/05
P	490537.58	4618470.19	10/06/05
P	490605.13	4618479.37	10/06/05
P	490552.47	4618482.92	10/06/05
P	490492.35	4618487.29	10/06/05
P	486590.00	4618491.00	29/04/05
P	490560.44	4618493.64	10/06/05
P	490474.33	4618495.86	10/06/05
P	490621.25	4618500.54	10/06/05
P	490020.45	4618511.85	30/05/05
P	490648.53	4618524.30	10/06/05
P	490578.82	4618525.52	10/06/05
P	490631.68	4618527.28	10/06/05
P	490585.86	4618532.56	10/06/05
A	480446.96	4618534.21	23/05/05
P	490589.81	4618538.35	10/06/05
P	486665.00	4618542.00	29/04/05
P	490357.16	4618542.19	30/05/05
P	490599.77	4618545.28	10/06/05
P	490603.23	4618548.20	10/06/05
P	490674.49	4618550.17	10/06/05
P	490726.77	4618575.18	10/06/05
A	490624.99	4618576.35	10/06/05
A	490737.04	4618587.03	10/06/05
P	490517.02	4618588.74	10/06/05
P	490635.97	4618592.72	10/06/05
P	490746.89	4618592.82	10/06/05
A	490758.39	4618600.03	10/06/05
A	490769.07	4618610.81	10/06/05
A	490647.90	4618613.97	10/06/05
P	490404.41	4618617.28	30/05/05
P	490305.06	4618618.06	30/05/05
A	490784.67	4618618.84	10/06/05

Pres Lh	*Longitude*	*Latitude*	*Date*
P	485943.00	4618628.00	29/04/05
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P	490530.44	4618629.73	10/06/05
A	490807.99	4618643.88	10/06/05
P	490538.44	4618644.31	10/06/05
A	490669.10	4618652.51	10/06/05
A	490248.88	4618653.63	?/07/04
P	490542.62	4618654.49	10/06/05
A	490819.99	4618659.95	10/06/05
A	490688.43	4618660.86	10/06/05
P	490555.45	4618679.31	10/06/05
A	490837.08	4618680.31	10/06/05
P	490353.01	4618681.03	30/05/05
A	490717.83	4618681.42	10/06/05
A	490735.25	4618688.02	10/06/05
P	490550.25	4618691.25	10/06/05
A	490756.73	4618714.75	10/06/05
P	490364.50	4618715.16	?/07/04
A	490595.37	4618740.00	10/06/05
A	490618.29	4618753.50	10/06/05
A	490737.80	4618757.93	10/06/05
P	490425.67	4618769.62	30/05/05
P	490452.59	4618771.48	30/05/05
P	490519.31	4618782.35	30/05/05
A	490557.50	4618785.28	10/06/05
A	490624.63	4618785.33	10/06/05
A	490617.55	4618786.55	30/05/05
A	490741.82	4618793.47	10/06/05
P	490387.25	4618806.98	30/05/05
A	490741.53	4618821.57	10/06/05
P	492190.06	4618836.30	?/07/04
A	490734.76	4618845.92	10/06/05
A	490754.51	4618847.04	10/06/05
A	490730.84	4618848.78	10/06/05
A	490750.30	4618855.84	10/06/05
A	490757.15	4618855.95	10/06/05
A	490790.08	4618862.24	10/06/05
A	490645.95	4618864.81	10/06/05
A	490670.50	4618866.87	10/06/05
A	490604.80	4618872.37	10/06/05
A	490396.92	4618881.33	10/06/05
P	490318.53	4618900.27	?/07/04
A	490594.38	4618901.07	10/06/05
A	490543.27	4618909.63	10/06/05
A	490395.72	4618913.14	10/06/05
P	486242.00	4618928.00	29/04/05
A	490406.47	4618929.84	10/06/05
A	490405.34	4618932.21	10/06/05
A	490535.35	4618932.50	10/06/05
P	488839.79	4618933.26	?/07/04
A	490519.59	4618938.42	10/06/05
A	490413.32	4618938.68	10/06/05
A	490419.43	4618940.22	10/06/05
A	490513.05	4618952.16	10/06/05
A	490492.17	4618968.76	10/06/05
A	490441.64	4618968.84	10/06/05
A	490471.77	4618971.90	10/06/05
P	486379.00	4619031.00	29/04/05
P	489949.05	4619054.98	?/07/04
P	489602.51	4619086.31	?/07/04
A	489487.03	4619117.32	?/07/04
A	487186.00	4619164.00	29/04/05
A	486899.33	4619183.27	?/07/04
P	486571.00	4619194.00	29/04/05
P	489995.48	4619209.12	?/07/04
P	489001.96	4619210.57	?/07/04
A	486905.00	4619218.00	29/04/05
A	486635.00	4619280.00	29/04/05
P	485581.36	4619290.58	25/05/05
A	489857.02	4619332.68	?/07/04
A	486726.00	4619339.00	29/04/05
A	485572.57	4619413.56	25/05/05
A	489164.02	4619426.21	?/07/04
A	489649.26	4619456.34	?/07/04
A	489418.21	4619456.67	?/07/04
A	485622.57	4619476.45	25/05/05
P	493784.96	4619482.39	?/07/04
A	489418.31	4619518.36	?/07/04
A	488956.22	4619519.05	?/07/04
P	492304.00	4619569.00	28/04/05
A	485862.83	4619579.58	25/05/05
A	485770.62	4619582.44	25/05/05
P	494940.26	4619604.85	?/07/04
A	484952.99	4619616.72	25/05/05
A	487125.00	4619618.00	29/04/05
P	492343.00	4619623.00	28/04/05
P	492271.00	4619635.00	28/04/05
P	484649.00	4619646.00	29/04/05
A	492424.00	4619665.00	28/04/05
P	492217.00	4619671.00	28/04/05
A	491434.00	4619673.00	28/04/05
A	492480.00	4619684.00	28/04/05
P	491739.00	4619716.00	28/04/05
P	492347.00	4619726.00	28/04/05
A	489141.38	4619734.66	?/07/04
A	484881.30	4619748.51	25/05/05
A	492283.48	4619761.42	?/07/04
A	489326.26	4619765.22	?/07/04
P	491682.00	4619775.00	28/04/05
P	492376.00	4619803.00	28/04/05
A	491143.00	4619811.00	28/04/05
P	494732.48	4619820.88	?/07/04
P	492422.17	4619822.95	?/07/04
P	492439.00	4619840.00	28/04/05
A	485834.15	4619850.20	25/05/05
A	484673.00	4619896.00	29/04/05
P	492383.00	4619919.00	28/04/05
A	495217.73	4619943.91	?/07/04

Pres Lh	*Longitude*	*Latitude*	*Date*
P	493669.85	4619945.11	?/07/04
A	491683.01	4619947.14	?/07/04
A	491671.00	4619961.00	28/04/05
P	493679.00	4619970.00	28/04/05
P	493230.93	4619976.35	?/07/04
A	492976.83	4620007.43	?/07/04
A	493092.37	4620038.16	?/07/04
A	485845.62	4620043.52	25/05/05
P	493761.00	4620070.00	28/04/05
P	485377.57	4620089.93	25/05/05
A	495934.04	4620159.35	?/07/04
P	493854.86	4620160.83	?/07/04
A	485684.75	4620175.20	25/05/05
P	492681.00	4620186.00	28/04/05
P	492653.58	4620192.80	?/07/04
P	492621.00	4620234.00	28/04/05
A	485551.06	4620254.51	25/05/05
P	492562.00	4620300.00	28/04/05
P	492606.00	4620306.00	28/04/05
A	485500.02	4620316.53	25/05/05
P	494062.95	4620376.54	?/07/04
P	493808.87	4620407.60	?/07/04
A	493785.84	4620500.14	?/07/04
A	494271.01	4620561.42	?/07/04
A	493739.70	4620561.86	?/07/04
A	494455.87	4620622.95	?/07/04
P	495634.03	4620683.82	?/07/04
P	495541.63	4620683.88	?/07/04
P	495934.39	4620776.17	?/07/04
P	495749.59	4620776.27	?/07/04
A	481823.33	4620835.23	23/05/05
P	495680.33	4620838.00	?/07/04
A	495726.55	4620868.81	?/07/04
P	495472.45	4620868.97	?/07/04
A	496096.17	4620930.28	?/07/04
P	484863.00	4620944.00	15/07/04
A	495819.00	4620961.28	?/07/04
A	495888.31	4620992.08	?/07/04
P	485073.00	4621034.00	09/08/04
A	485234.00	4621055.00	15/07/04
A	491506.00	4621100.00	28/04/05
A	496165.57	4621115.29	?/07/04
A	485181.00	4621135.00	15/07/04
P	481704.47	4621138.26	23/05/05
P	485016.00	4621140.00	15/07/04
A	495934.60	4621146.26	?/07/04
P	491423.00	4621152.00	28/04/05
A	485340.00	4621156.00	09/08/04
P	484980.00	4621183.00	15/07/04
A	486587.00	4621213.00	09/08/04
P	485026.00	4621236.00	09/08/04
A	496489.05	4621300.17	?/07/04
P	491502.00	4621329.00	28/04/05
P	491546.00	4621337.00	28/04/05
A	496650.80	4621423.45	?/07/04
P	496373.70	4621577.79	?/07/04
P	481471.51	4621598.81	23/05/05
A	485766.00	4621618.00	09/08/04
A	486411.00	4621658.00	09/08/04
P	481306.96	4621739.13	23/05/05
A	496997.42	4621793.39	?/07/04
P	481291.78	4621849.37	23/05/05
A	496674.15	4621978.58	?/07/04
P	481333.64	4622036.87	23/05/05
A	483007.00	4622079.00	15/07/04
A	482886.00	4622100.00	15/07/04
A	496466.35	4622102.04	?/07/04
P	481269.00	4622121.00	23/05/05
A	482989.24	4622124.28	23/05/05
P	481252.66	4622177.11	23/05/05
A	483370.00	4622301.00	15/07/04
A	497344.07	4622317.55	?/07/04
A	483489.36	4622319.71	23/05/05
A	483072.00	4622335.00	15/07/04
A	482757.52	4622366.52	23/05/05
A	484206.00	4622461.00	15/07/04
A	482752.00	4622472.00	15/07/04
A	483228.02	4622484.51	23/05/05
A	483591.00	4622501.00	15/07/04
A	482707.85	4622631.63	23/05/05
A	483395.00	4622636.30	23/05/05
A	482609.66	4622638.58	23/05/05
A	481696.62	4622684.00	25/05/05
A	482637.00	4622709.00	15/07/04
A	497020.90	4622718.61	?/07/04
A	497852.30	4622779.99	?/07/04
A	497436.62	4622810.97	?/07/04
A	497841.00	4622831.00	06/05/05
A	497870.00	4622856.00	06/05/05
A	497436.65	4622872.65	?/07/04
A	497900.00	4622893.00	06/05/05
A	497854.00	4622903.00	06/05/05
A	497898.53	4622934.18	?/07/04
A	481657.91	4622980.28	25/05/05
A	497839.00	4622993.00	06/05/05
A	481916.00	4623006.00	15/07/04
A	482109.60	4623045.26	23/05/05
A	482077.82	4623098.25	23/05/05
A	498060.23	4623119.18	?/07/04
A	482022.87	4623125.73	23/05/05
A	482040.00	4623136.00	15/07/04
A	498074.00	4623147.00	06/05/05
P	498129.52	4623150.00	?/07/04
A	497713.85	4623150.13	?/07/04
A	482195.00	4623169.00	15/07/04
P	498082.00	4623173.00	06/05/05
A	481915.00	4623176.00	15/07/04
P	498037.16	4623180.87	?/07/04

Pres Lh	*Longitude*	*Latitude*	*Date*
A	481914.00	4623189.00	15/07/04
P	498161.00	4623207.00	06/05/05
P	498152.62	4623211.68	?/07/04
P	481928.00	4623230.00	15/07/04
P	498085.00	4623243.00	06/05/05
P	482009.00	4623269.00	15/07/04
P	498004.00	4623275.00	06/05/05
A	482107.00	4623278.00	15/07/04
A	482107.00	4623296.00	15/07/04
P	497949.00	4623325.00	06/05/05
P	497942.00	4623399.00	06/05/05
P	497898.67	4623427.64	?/07/04
A	490490.00	4623437.00	28/04/05
P	497898.75	4623674.37	?/07/04
P	497644.77	4623736.13	?/07/04
P	497852.60	4623797.74	?/07/04
P	497806.45	4623890.28	?/07/04
A	497621.73	4623890.34	?/07/04
A	490688.00	4623912.00	28/04/05
P	498637.72	4624044.28	?/07/04
A	481811.00	4624055.00	15/07/04
A	489396.00	4624799.00	28/04/05
A	483426.00	4625222.00	15/07/04
A	481634.00	4625464.00	15/07/04
A	498938.10	4625524.60	?/07/04
P	481578.00	4625529.00	15/07/04
A	498776.52	4625555.47	?/07/04
P	481128.00	4625636.00	15/07/04
A	499030.46	4625647.95	?/07/04
P	481658.00	4625663.00	15/07/04
A	482946.00	4625699.00	15/07/04
P	481616.00	4625801.00	15/07/04
P	498891.98	4625802.18	?/07/04
A	481001.00	4625820.00	15/07/04
A	481103.00	4625823.00	15/07/04
P	481333.00	4625860.00	15/07/04
P	481341.00	4625878.00	15/07/04
A	488634.00	4625891.00	28/04/05
A	481193.00	4625907.00	15/07/04
A	480809.00	4625931.00	15/07/04
P	499053.60	4626048.88	?/07/04
P	501838.00	4626139.00	02/08/04
A	488740.00	4626147.00	28/04/05
P	500991.00	4626152.00	02/08/04
P	500854.06	4626172.23	?/07/04
A	482162.04	4626178.28	11/07/05
A	482641.00	4626194.00	15/07/04
P	500738.00	4626208.00	02/08/04
P	499492.19	4626233.88	?/07/04
P	501711.00	4626236.00	02/08/04
A	481620.00	4626247.00	15/07/04
P	499422.94	4626264.73	?/07/04
P	499944.00	4626283.00	02/08/04
P	500184.66	4626326.39	?/07/04
P	501384.00	4626354.00	02/08/04
P	501607.00	4626366.00	02/08/04
P	501586.00	4626409.00	02/08/04
A	481454.83	4626416.00	11/07/05
P	499607.61	4626449.76	?/07/04
A	498661.26	4626449.88	?/07/04
A	482951.39	4626521.57	11/07/05
P	499422.97	4626573.14	?/07/04
A	499215.24	4626604.00	?/07/04
A	498707.46	4626665.76	?/07/04
P	499376.81	4626696.51	?/07/04
A	483049.00	4626720.00	15/07/04
A	498938.28	4626727.40	?/07/04
A	498638.23	4626727.45	?/07/04
P	481525.47	4626745.36	11/07/05
A	499169.09	4626758.21	?/07/04
P	499538.39	4626789.02	?/07/04
P	499469.15	4626819.87	?/07/04
A	483695.72	4626857.72	11/07/05
P	501502.00	4626900.00	02/08/04
P	500990.00	4626935.00	02/08/04
P	501246.00	4626971.00	02/08/04
P	500655.00	4626984.00	02/08/04
P	500440.00	4627074.00	02/08/04
A	481539.57	4627120.75	11/07/05
P	499699.97	4627128.26	?/07/04
A	484342.92	4627153.88	11/07/05
P	501010.00	4627192.00	02/08/04
P	500796.00	4627222.00	02/08/04
P	502919.00	4627226.00	02/08/04
A	484094.00	4627246.00	15/07/04
A	487177.00	4627271.00	15/07/04
P	501140.00	4627300.00	02/08/04
A	487143.00	4627303.00	15/07/04
A	484590.00	4627304.00	15/07/04
A	484111.00	4627396.00	15/07/04
A	487411.00	4627426.00	15/07/04
A	483909.00	4627445.00	15/07/04
A	477664.00	4627459.00	?/06/04
A	487150.00	4627464.00	15/07/04
P	503578.00	4627475.00	02/08/04
P	501057.00	4627505.00	02/08/04
A	487282.00	4627549.00	15/07/04
P	504088.00	4627560.00	09/08/04
P	503806.00	4627562.00	09/08/04
A	487289.00	4627587.00	15/07/04
A	481345.33	4627596.97	11/07/05
A	487419.00	4627600.00	15/07/04
P	500719.00	4627610.00	02/08/04
P	500738.49	4627621.75	?/07/04
P	501163.00	4627626.00	02/08/04
P	487601.00	4627636.00	15/07/04
A	487066.00	4627650.00	?/06/04
P	500900.04	4627652.61	?/07/04

Pres Lh	*Longitude*	*Latitude*	*Date*
A	487739.00	4627673.00	15/07/04
A	486682.00	4627700.00	15/07/04
A	485684.66	4627710.39	11/07/05
A	488803.00	4627714.00	28/04/05
A	487393.00	4627735.00	15/07/04
P	487643.00	4627758.00	15/07/04
P	503829.00	4627795.00	09/08/04
A	487591.00	4627866.00	15/07/04
A	497738.44	4627868.80	?/07/04
P	499149.00	4627890.00	06/05/05
A	486595.00	4627896.00	15/07/04
P	487854.00	4627918.00	15/07/04
A	487027.00	4627921.00	15/07/04
A	486357.53	4627930.71	11/07/05
A	487211.00	4627931.00	15/07/04
A	487938.00	4627931.00	?/06/04
P	487242.00	4627977.00	15/07/04
A	486628.15	4627996.37	11/07/05
A	486624.00	4627999.00	15/07/04
A	487959.00	4628004.00	15/07/04
P	486515.00	4628017.00	15/07/04
A	487965.00	4628022.00	15/07/04
A	497807.72	4628022.99	?/07/04
A	481051.87	4628026.08	11/07/05
P	497853.88	4628053.82	?/07/04
P	487329.00	4628090.00	?/06/04
A	488134.00	4628098.00	15/07/04
P	503522.00	4628098.00	09/08/04
P	487354.70	4628105.47	11/07/05
A	477683.00	4628110.00	?/06/04
P	487359.00	4628121.00	15/07/04
A	488013.00	4628123.00	15/07/04
P	504218.00	4628171.00	09/08/04
P	499330.79	4628176.89	?/07/04
P	503797.00	4628186.00	09/08/04
P	503840.00	4628194.00	09/08/04
A	480637.66	4628194.19	11/07/05
A	477950.50	4628195.00	11/07/05
A	478962.00	4628199.00	?/06/04
P	487668.00	4628201.00	?/06/04
A	480355.71	4628216.62	11/07/05
P	487945.00	4628227.00	15/07/04
P	503400.00	4628228.00	09/08/04
P	487115.00	4628229.00	?/06/04
P	487358.00	4628230.00	15/07/04
A	478626.00	4628230.00	28/04/05
P	487423.00	4628231.00	?/06/04
P	487891.00	4628231.00	?/06/04
A	497530.87	4628238.97	?/07/04
P	487139.00	4628245.00	15/07/04
P	503869.00	4628250.00	09/08/04
P	504448.00	4628253.00	09/08/04
A	478933.08	4628254.18	02/06/05
A	478668.00	4628261.00	28/04/05
P	487945.00	4628262.00	28/04/05
P	478668.00	4628263.00	28/04/05
A	478395.00	4628267.00	28/04/05
A	477573.07	4628269.54	11/07/05
P	498015.48	4628269.66	?/07/04
P	487930.00	4628270.00	15/07/04
A	492361.89	4628273.47	?/07/04
A	478666.00	4628281.00	28/04/05
P	503313.00	4628282.00	09/08/04
P	487827.00	4628283.00	15/07/04
P	487111.00	4628291.00	?/06/04
P	487904.00	4628297.00	15/07/04
A	478276.96	4628297.71	11/07/05
P	478700.00	4628298.00	28/04/05
P	499307.73	4628300.26	?/07/04
P	478751.00	4628303.00	28/04/05
P	487912.34	4628303.76	11/07/05
P	478765.00	4628305.00	28/04/05
P	478715.00	4628308.00	28/04/05
A	488013.69	4628312.07	11/07/05
P	478814.00	4628318.00	?/06/04
A	486388.00	4628328.00	15/07/04
P	497946.27	4628331.36	?/07/04
P	478849.00	4628332.00	?/06/04
A	478472.00	4628332.00	28/04/05
P	478872.00	4628333.00	?/06/04
P	479000.00	4628335.00	28/04/05
P	503937.00	4628336.00	09/08/04
A	486621.00	4628341.00	15/07/04
A	486866.00	4628341.00	15/07/04
P	478980.00	4628343.00	28/04/05
A	478366.00	4628344.00	28/04/05
P	487873.00	4628347.00	15/07/04
P	488033.00	4628357.00	15/07/04
P	478520.00	4628366.00	28/04/05
P	478864.00	4628366.00	28/04/05
P	478909.00	4628369.00	?/06/04
A	488099.19	4628372.06	11/07/05
P	478544.00	4628379.00	28/04/05
P	478589.00	4628385.00	?/06/04
A	478469.94	4628387.19	11/07/05
P	487813.00	4628411.00	15/07/04
P	478598.00	4628414.00	?/06/04
P	478602.17	4628414.18	11/07/05
P	503280.00	4628421.00	09/08/04
P	478590.00	4628429.00	?/06/04
A	486958.00	4628434.00	15/07/04
P	478890.00	4628446.00	?/06/04
P	486988.00	4628453.00	15/07/04
A	497646.32	4628454.82	?/07/04
P	487027.00	4628457.00	?/06/04
P	478815.00	4628461.00	?/06/04
P	487022.00	4628465.00	15/07/04
P	478928.00	4628480.00	?/06/04

Pres Lh	*Longitude*	*Latitude*	*Date*
P	500023.08	4628485.27	?/07/04
P	479422.33	4628486.94	11/07/05
P	478838.00	4628501.00	?/06/04
P	478850.00	4628505.00	?/06/04
P	503958.00	4628509.00	09/08/04
P	487283.00	4628545.00	15/07/04
P	487653.00	4628545.00	15/07/04
A	499400.05	4628546.98	?/07/04
P	478946.28	4628548.08	02/06/05
A	491739.17	4628551.73	?/07/04
P	478937.00	4628563.00	?/06/04
P	478904.22	4628563.20	11/07/05
P	487474.00	4628565.00	?/06/04
P	479139.45	4628576.04	11/07/05
A	497738.67	4628608.99	?/07/04
P	503245.00	4628620.00	09/08/04
P	487728.00	4628664.00	15/07/04
A	477427.40	4628675.15	11/07/05
P	500360.00	4628679.00	02/08/04
P	497831.00	4628701.49	?/07/04
P	487607.00	4628723.00	15/07/04
A	487693.00	4628745.00	15/07/04
A	487729.00	4628745.00	15/07/04
A	488657.35	4628753.67	11/07/05
P	504092.00	4628756.00	09/08/04
A	489719.61	4628760.85	11/07/05
A	488576.00	4628761.00	15/07/04
P	499472.00	4628768.00	06/05/05
A	486285.00	4628786.00	15/07/04
A	489309.43	4628806.85	11/07/05
A	490811.68	4628808.80	11/07/05
A	486210.00	4628810.00	15/07/04
P	499352.00	4628847.00	03/08/04
A	499076.00	4628855.00	03/08/04
P	504130.00	4628884.00	09/08/04
P	499323.00	4628896.00	03/08/04
A	477330.43	4628969.47	11/07/05
P	502945.00	4628978.00	02/08/04
A	487746.00	4628997.00	15/07/04
P	504239.00	4629011.00	09/08/04
P	501985.00	4629014.00	02/08/04
P	503621.00	4629053.00	09/08/04
P	499651.00	4629054.00	03/08/04
P	498864.00	4629059.00	03/08/04
P	503808.00	4629066.00	09/08/04
A	477280.45	4629085.47	11/07/05
P	503035.00	4629094.00	02/08/04
A	498603.00	4629195.00	03/08/04
A	498185.00	4629220.00	03/08/04
A	496769.81	4629226.19	?/07/04
P	503083.00	4629263.00	02/08/04
A	498075.00	4629279.00	03/08/04
A	496885.20	4629287.82	?/07/04
P	501896.00	4629288.00	02/08/04
A	496942.00	4629309.00	03/08/04
P	502220.00	4629330.00	02/08/04
P	503329.00	4629338.00	02/08/04
P	504241.00	4629342.00	09/08/04
P	501923.00	4629398.00	02/08/04
P	502168.00	4629409.00	02/08/04
A	497208.27	4629411.05	?/07/04
A	497231.34	4629411.05	?/07/04
P	503250.00	4629431.00	02/08/04
P	497283.00	4629443.00	03/08/04
P	504469.00	4629466.00	09/08/04
A	477165.75	4629527.82	11/07/05
P	499290.29	4629602.24	11/07/05
A	495642.00	4629613.00	22/04/05
P	500641.00	4629625.00	02/08/04
P	504554.00	4629689.00	09/08/04
A	499448.00	4629800.00	22/04/05
A	476966.09	4629850.53	11/07/05
A	476193.00	4629873.00	28/04/05
A	491950.31	4629884.65	11/07/05
P	499636.89	4629905.26	11/07/05
P	504459.00	4629906.00	09/08/04
P	500670.00	4629919.00	02/08/04
P	500595.00	4629920.00	02/08/04
A	499010.91	4629964.71	11/07/05
P	504562.00	4630009.00	09/08/04
P	504662.00	4630079.00	09/08/04
P	492201.97	4630103.51	11/07/05
A	476848.38	4630148.23	11/07/05
A	497623.82	4630181.94	?/07/04
P	504780.00	4630193.00	09/08/04
A	498475.00	4630199.00	22/04/05
A	492489.70	4630204.93	11/07/05
P	504926.00	4630231.00	09/08/04
A	498540.67	4630248.17	11/07/05
P	476440.00	4630258.00	28/04/05
A	476350.00	4630261.00	28/04/05
P	499705.75	4630277.90	11/07/05
P	476441.00	4630281.00	28/04/05
P	476474.00	4630283.00	?/06/04
P	500947.00	4630283.00	06/05/05
A	476011.00	4630296.00	28/04/05
A	476329.00	4630298.00	28/04/05
A	475952.26	4630326.69	18/05/05
P	500909.00	4630338.00	06/05/05
A	476377.00	4630354.00	28/04/05
P	500839.00	4630362.00	06/05/05
P	500785.00	4630367.00	06/05/05
P	498206.32	4630384.14	11/07/05
P	500784.00	4630396.00	06/05/05
P	499848.00	4630410.00	22/04/05
A	498497.00	4630414.95	11/07/05
P	504921.00	4630507.00	09/08/04
A	493206.84	4630539.25	11/07/05

Pres Lh	*Longitude*	*Latitude*	*Date*
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A	496023.00	4630570.00	22/04/05
P	495883.00	4630574.00	22/04/05
P	500014.00	4630586.00	22/04/05
P	495948.00	4630587.00	22/04/05
A	496023.00	4630615.00	22/04/05
P	495747.00	4630623.00	22/04/05
P	501954.48	4630628.30	22/06/05
P	495736.00	4630646.00	22/04/05
P	501942.36	4630650.05	22/06/05
P	495663.00	4630661.00	22/04/05
A	501920.41	4630663.21	22/06/05
A	501956.00	4630668.82	22/06/05
P	504457.00	4630669.00	09/08/04
P	495738.00	4630670.00	22/04/05
P	499991.02	4630674.36	11/07/05
P	504097.00	4630710.00	09/08/04
P	495791.00	4630716.00	22/04/05
A	501888.53	4630718.79	22/06/05
P	504465.00	4630736.00	09/08/04
P	500151.00	4630742.00	22/04/05
P	495654.00	4630763.00	22/04/05
P	495654.00	4630763.00	22/04/05
P	495654.00	4630763.00	22/04/05
A	475666.34	4630763.59	18/05/05
A	484529.00	4630764.00	15/07/04
P	500196.00	4630793.00	22/04/05
P	504849.00	4630802.00	09/08/04
P	496229.68	4630808.08	11/07/05
P	495689.93	4630816.41	11/07/05
P	496605.94	4630844.92	11/07/05
P	500537.44	4630850.11	22/06/05
A	500636.65	4630859.85	22/06/05
P	495439.35	4630861.62	11/07/05
A	500654.10	4630869.05	22/06/05
P	496935.09	4630880.54	11/07/05
A	493923.14	4630888.97	11/07/05
P	505917.00	4630893.00	09/08/04
A	485430.00	4630915.00	15/07/04
P	504740.00	4630945.00	09/08/04
P	498404.00	4630976.00	22/04/05
P	504564.00	4630993.00	09/08/04
P	498703.44	4631023.16	22/06/05
P	498826.48	4631038.04	22/06/05
P	504793.00	4631049.00	09/08/04
P	499963.00	4631049.00	22/04/05
P	504318.00	4631066.00	09/08/04
P	498600.36	4631068.28	22/06/05
P	499942.00	4631079.00	22/04/05
A	485243.00	4631083.00	15/07/04
A	475457.66	4631100.54	18/05/05
P	490963.37	4631121.94	19/05/05
P	498463.04	4631127.33	22/06/05
P	498980.08	4631139.88	22/06/05
A	490606.44	4631159.72	19/05/05
P	504583.00	4631178.00	09/08/04
P	499036.86	4631178.30	22/06/05
P	499440.74	4631213.86	22/06/05
P	490933.18	4631220.19	19/05/05
A	490592.41	4631231.08	27/06/05
P	504126.00	4631248.00	09/08/04
P	499102.75	4631260.98	22/06/05
P	499454.81	4631271.69	22/06/05
A	490577.05	4631281.49	27/06/05
P	500994.52	4631283.37	22/06/05
P	490572.70	4631294.87	27/06/05
A	490569.49	4631311.01	27/06/05
P	490613.39	4631315.15	19/05/05
P	499365.78	4631315.34	22/06/05
P	506037.00	4631318.00	09/08/04
A	485311.00	4631321.00	15/07/04
A	490567.53	4631322.40	27/06/05
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P	498507.00	4631351.00	22/04/05
P	498432.00	4631355.00	22/04/05
P	501139.24	4631355.72	22/06/05
P	490580.07	4631357.85	19/05/05
P	499433.45	4631364.13	22/06/05
A	490546.77	4631375.02	27/06/05
P	490521.69	4631390.80	27/06/05
P	490899.82	4631399.15	19/05/05
A	490531.36	4631417.42	27/06/05
P	499499.07	4631426.52	22/06/05
P	499521.17	4631437.60	22/06/05
P	499509.06	4631440.35	22/06/05
A	490520.64	4631441.13	27/06/05
P	498622.00	4631446.00	22/04/05
P	499530.88	4631447.72	22/06/05
A	490509.87	4631453.78	27/06/05
A	490511.52	4631456.40	27/06/05
P	499548.87	4631465.60	22/06/05
A	490502.17	4631465.79	19/05/05
A	490500.51	4631471.03	27/06/05
P	491051.69	4631474.34	19/05/05
A	484283.00	4631479.00	15/07/04
P	504534.00	4631480.00	09/08/04
A	490481.22	4631500.05	27/06/05
A	490475.94	4631505.66	27/06/05
P	490502.94	4631509.41	27/06/05
A	474975.06	4631510.18	18/05/05
A	490458.57	4631537.89	19/05/05
A	490455.82	4631542.38	27/06/05
A	490440.82	4631547.05	27/06/05
A	490429.24	4631555.26	27/06/05
P	490491.59	4631557.10	27/06/05
P	501552.53	4631570.40	22/06/05
P	490445.42	4631594.35	27/06/05
A	490409.60	4631595.64	27/06/05

Pres Lh	Longitude	Latitude	Date
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P	501479.38	4631615.33	22/06/05
A	501325.00	4631617.06	22/06/05
P	490442.81	4631617.81	27/06/05
P	501628.38	4631630.56	22/06/05
A	490381.21	4631633.40	27/06/05
P	501469.92	4631645.34	22/06/05
P	490443.40	4631645.93	27/06/05
A	490362.81	4631653.58	19/05/05
P	490458.61	4631655.39	27/06/05
P	490438.45	4631681.32	27/06/05
P	490448.91	4631687.24	27/06/05
P	490439.56	4631711.22	27/06/05
A	490436.77	4631737.97	27/06/05
A	490432.28	4631751.56	27/06/05
A	501172.30	4631753.48	22/06/05
A	490456.76	4631753.87	27/06/05
A	504545.00	4631767.00	09/08/04
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A	490064.96	4631885.07	19/05/05
A	501197.84	4631895.53	22/06/05
A	504534.00	4631896.00	09/08/04
P	504549.00	4631901.00	09/08/04
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A	485576.00	4631912.00	15/07/04
A	474595.60	4631920.64	18/05/05
P	507329.00	4631959.00	09/08/04
P	505770.00	4631970.00	09/08/04
P	501268.22	4632004.79	22/06/05
A	501074.90	4632050.99	22/06/05
P	507082.00	4632065.00	09/08/04
P	490830.75	4632070.66	19/05/05
P	490695.43	4632092.68	19/05/05
A	490649.18	4632099.11	19/05/05
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A	489665.15	4632147.42	19/05/05
A	500570.78	4632149.56	22/06/05
P	506867.00	4632152.00	09/08/04
P	505891.00	4632244.00	09/08/04
A	484832.00	4632287.00	15/07/04
P	506623.00	4632389.00	09/08/04
P	499033.00	4632443.00	22/04/05
P	505999.00	4632574.00	09/08/04
A	473911.80	4632619.91	18/05/05
P	498875.00	4632621.00	22/04/05
P	498873.00	4632630.00	22/04/05
P	498535.00	4632800.00	22/04/05
P	498711.00	4632817.00	22/04/05
A	499488.51	4632824.46	22/06/05
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P	499020.00	4632992.00	22/04/05
P	506274.00	4632993.00	09/08/04
P	503858.00	4633058.00	13/05/05
P	503633.00	4633065.00	13/05/05
P	503695.00	4633086.00	13/05/05
P	498517.00	4633087.00	22/04/05
A	473343.81	4633091.60	18/05/05
P	506306.00	4633099.00	13/05/05
P	498637.00	4633139.00	22/04/05
P	506267.00	4633147.00	09/08/04
P	498847.00	4633300.00	22/04/05
A	503669.00	4633335.00	13/05/05
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P	508707.00	4633531.00	22/07/04
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A	499066.00	4633534.00	22/04/05
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P	506374.00	4633594.00	09/08/04
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A	490708.81	4633663.06	19/05/05
A	502955.00	4633679.00	13/05/05
P	498832.60	4633721.20	22/06/05
P	504093.00	4633726.00	13/05/05
A	497812.17	4633757.43	01/07/05
A	497957.00	4633764.00	22/04/05
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A	502543.00	4633781.00	13/05/05
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P	510433.00	4633807.00	29/07/04
A	497646.42	4633817.04	01/07/05
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A	497943.08	4633851.22	22/06/05
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P	510383.00	4633892.00	29/07/04
A	497692.77	4633917.32	01/07/05
A	507069.00	4633927.00	22/07/04
A	472860.37	4633927.27	18/05/05
A	498898.00	4633933.00	13/05/05
A	501358.00	4633944.00	13/05/05
A	498704.97	4633951.65	22/06/05
P	504099.00	4633959.00	13/05/05
A	498728.00	4633968.00	22/04/05
P	504540.00	4633973.00	13/05/05
A	472619.20	4633996.01	18/05/05
P	497971.47	4634016.81	22/06/05
P	506927.00	4634040.00	22/07/04
A	502134.00	4634043.00	13/05/05
P	497886.71	4634069.86	22/06/05

Pres Lh	*Longitude*	*Latitude*	*Date*
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A	498450.00	4634088.00	22/04/05
P	497950.31	4634088.78	22/06/05
P	498005.12	4634110.16	22/06/05
P	497984.11	4634114.00	22/06/05
P	497986.56	4634116.68	22/06/05
P	498027.35	4634118.42	22/06/05
P	497914.34	4634125.66	22/06/05
P	504518.00	4634137.00	13/05/05
A	490594.91	4634141.72	19/05/05
P	497966.34	4634149.72	22/06/05
A	498205.45	4634149.82	01/07/05
A	499193.00	4634153.00	13/05/05
P	498014.45	4634158.25	22/06/05
P	498155.25	4634159.77	01/07/05
P	498007.12	4634162.25	22/06/05
P	498014.68	4634168.99	22/06/05
P	498017.73	4634171.26	22/06/05
P	498022.23	4634176.90	22/06/05
P	498020.95	4634186.72	22/06/05
P	498057.75	4634199.24	22/06/05
P	510146.00	4634203.00	22/07/04
P	498079.66	4634206.00	22/06/05
P	498099.83	4634210.57	22/06/05
P	510495.00	4634213.00	29/07/04
P	497858.91	4634216.58	01/07/05
P	497879.23	4634225.06	01/07/05
P	510191.00	4634233.00	29/07/04
P	504703.00	4634240.00	13/05/05
P	509697.00	4634275.00	22/07/04
P	508339.00	4634280.00	22/07/04
A	507485.00	4634284.00	22/07/04
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A	500929.00	4634444.00	13/05/05
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P	508333.00	4634490.00	22/07/04
P	510117.00	4634516.00	29/07/04
P	512524.00	4634517.00	21/07/04
A	490224.50	4634529.72	19/05/05
P	508731.00	4634530.00	22/07/04
P	510078.00	4634531.00	29/07/04
P	508031.00	4634531.00	22/07/04
P	510090.00	4634536.00	29/07/04
P	505540.00	4634537.00	13/05/05
A	507575.00	4634540.00	22/07/04
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A	500379.00	4634602.00	13/05/05
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P	512431.00	4634651.00	21/07/04
A	499753.00	4634717.00	13/05/05
P	510583.00	4634723.00	22/07/04
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P	497998.00	4634735.00	22/04/05
A	499692.00	4634743.00	13/05/05
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P	507975.00	4634790.00	22/07/04
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A	500860.00	4634954.00	13/05/05
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P	506074.00	4635552.00	13/05/05
P	510425.00	4635554.00	21/07/04
A	512974.00	4635564.00	21/07/04
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P	510133.00	4635573.00	22/07/04
A	510893.00	4635583.00	21/07/04
A	512023.00	4635591.00	21/07/04
P	510435.00	4635624.00	21/07/04
A	512614.00	4635634.00	21/07/04
P	505710.00	4635634.00	13/05/05

Pres Lh	Longitude	Latitude	Date
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P	512815.00	4635724.00	21/07/04
P	511028.00	4635736.00	22/07/04
A	490392.81	4635755.94	19/05/05
P	511106.00	4635805.00	22/07/04
P	512612.00	4635806.00	21/07/04
P	510199.00	4635814.00	21/07/04
P	512602.00	4635837.00	21/07/04
A	510848.00	4635865.00	21/07/04
P	510049.00	4635934.00	21/07/04
P	510830.00	4635979.00	21/07/04
P	510805.00	4636013.00	21/07/04
P	510061.00	4636040.00	21/07/04
P	505175.00	4636070.00	13/05/05
A	490321.04	4636071.69	19/05/05
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P	511165.00	4636116.00	21/07/04
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P	511850.00	4636275.00	21/07/04
P	511144.00	4636299.00	21/07/04
A	510081.00	4636299.00	22/07/04
P	511561.00	4636309.00	21/07/04
A	509983.00	4636340.00	22/07/04
P	505444.00	4636383.00	13/05/05
P	511162.00	4636433.00	21/07/04
A	510141.00	4636488.00	22/07/04
A	510793.00	4636500.00	21/07/04
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A	510478.00	4636672.00	21/07/04
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A	510247.00	4636791.00	22/07/04
P	514608.00	4636798.00	10/08/04
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A	490660.16	4636950.68	19/05/05
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P	514582.00	4636979.00	10/08/04
A	490441.69	4636994.08	19/05/05
A	510510.00	4637062.00	21/07/04
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P	514622.00	4637066.00	10/08/04
P	509891.00	4637087.00	21/07/04
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P	509963.00	4637305.00	21/07/04
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P	510549.00	4637719.00	21/07/04
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P	490646.56	4637947.34	20/05/05
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P	514428.00	4638031.00	10/08/04
A	488970.23	4638033.92	19/05/05
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P	512785.00	4638045.00	10/08/04
P	512877.00	4638045.00	10/08/04
P	512676.00	4638102.00	10/08/04

Pres Lh	*Longitude*	*Latitude*	*Date*
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A	488702.48	4638125.01	11/07/05
A	512504.00	4638136.00	10/08/04
A	514388.00	4638219.00	10/08/04
A	488254.20	4638225.16	11/07/05
A	491180.86	4638232.58	20/05/05
A	487997.92	4638233.43	11/07/05
P	514674.00	4638239.00	10/08/04
A	483652.36	4638240.26	11/07/05
A	491594.81	4638267.11	20/05/05
A	512749.00	4638296.00	10/08/04
A	512300.00	4638298.00	10/08/04
A	487462.39	4638337.34	11/07/05
P	514610.00	4638343.00	10/08/04
A	487182.32	4638351.74	11/07/05
A	483841.70	4638369.52	11/07/05
A	484238.68	4638397.97	11/07/05
P	513653.00	4638399.00	10/08/04
A	486911.42	4638405.43	11/07/05
A	491657.05	4638411.24	20/05/05
P	515020.00	4638442.00	10/08/04
P	516822.00	4638474.00	10/08/04
P	514350.00	4638501.00	10/08/04
A	486410.55	4638503.73	11/07/05
A	486011.68	4638538.71	11/07/05
A	485793.08	4638588.69	11/07/05
A	504811.00	4638593.00	13/05/05
A	484399.35	4638618.05	11/07/05
A	491892.95	4638621.76	20/05/05
P	516025.00	4638665.00	10/08/04
A	513764.00	4638674.00	10/08/04
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A	488163.25	4638732.89	19/05/05
A	488057.70	4638752.53	19/05/05
A	504566.00	4638755.00	13/05/05
A	484526.24	4638759.43	11/07/05
P	516868.00	4638772.00	10/08/04
P	488410.79	4638788.50	19/05/05
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P	488372.42	4638799.96	19/05/05
P	514239.00	4638843.00	10/08/04
P	512612.00	4638859.00	10/08/04
P	514213.00	4638876.00	10/08/04
P	488455.35	4638878.05	19/05/05
P	488495.72	4638924.28	19/05/05
A	504193.00	4638994.00	13/05/05
P	516721.00	4639007.00	10/08/04
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P	488952.28	4639049.49	27/06/05
P	489000.23	4639071.46	27/06/05
A	513922.00	4639088.00	10/08/04
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P	488682.33	4639100.63	19/05/05
P	489036.45	4639100.78	27/06/05
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P	489197.71	4639125.15	27/06/05
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P	489062.36	4639137.39	27/06/05
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A	489039.06	4639153.48	27/06/05
P	489153.29	4639155.54	27/06/05
P	489215.22	4639159.93	27/06/05
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A	489108.54	4639168.01	27/06/05
A	489063.49	4639168.60	27/06/05
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P	489133.16	4639178.19	27/06/05
P	489096.67	4639182.69	27/06/05
P	488849.36	4639186.31	19/05/05
P	488993.15	4639191.57	27/06/05
P	488959.74	4639199.55	27/06/05
A	489100.75	4639199.87	27/06/05
P	489109.24	4639200.11	27/06/05
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P	488910.38	4639233.72	27/06/05
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A	489138.48	4639244.21	27/06/05
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A	489174.78	4639258.01	27/06/05
A	489256.47	4639266.60	27/06/05
A	488997.78	4639286.37	27/06/05
A	489009.55	4639298.56	27/06/05
A	489016.38	4639299.06	27/06/05
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A	488979.78	4639314.46	27/06/05
A	488978.84	4639314.46	27/06/05
A	488985.63	4639328.41	19/05/05
P	515719.00	4639334.00	10/08/04
P	517232.00	4639341.00	10/08/04
A	492543.74	4639377.60	20/05/05
A	488083.82	4639380.22	19/05/05
A	489011.29	4639398.58	27/06/05
P	517099.00	4639401.00	10/08/04

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A	492643.09	4639748.75	20/05/05
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P	515856.00	4640070.00	10/08/04
P	516783.00	4640135.00	10/08/04
P	515119.00	4640222.00	10/08/04
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A	492621.25	4640668.24	20/05/05
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P	517546.00	4641337.00	12/08/04
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P	516953.00	4642520.00	12/08/04
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A	494405.27	4643059.58	20/05/05
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A	495184.82	4643207.03	20/05/05
A	495913.27	4643211.68	20/05/05
P	515257.00	4643213.00	12/08/04
A	497109.35	4643232.62	20/05/05
A	502540.00	4643360.00	13/05/05

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A	510448.09	4644048.94	06/07/05
P	510132.55	4644063.75	06/07/05
P	509603.61	4644073.15	06/07/05
P	509537.30	4644162.41	06/07/05
P	509834.06	4644176.11	06/07/05
A	509041.22	4644236.79	06/07/05
A	498058.49	4644340.84	20/05/05
A	510818.83	4644436.35	06/07/05
A	508013.37	4644491.80	06/07/05
A	507393.07	4644607.77	06/07/05
A	510833.12	4644697.83	06/07/05
A	510870.61	4644737.79	06/07/05
A	506898.08	4644745.53	06/07/05
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A	511062.03	4644890.29	06/07/05
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A	499851.06	4644967.90	20/05/05
A	498235.37	4644968.48	20/05/05
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A	503319.57	4645132.84	06/07/05
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A	504704.87	4645305.85	06/07/05
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P	516565.00	4647426.00	16/08/04
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P	516387.00	4647448.00	16/08/04
A	512705.15	4647490.70	06/07/05
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P	516327.00	4647792.00	16/08/04
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P	515173.00	4647870.00	16/08/04
P	517108.00	4647889.00	08/09/04
P	516203.00	4647936.00	16/08/04
P	516663.00	4647989.00	08/09/04
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P	515070.00	4648181.00	16/08/04
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A	512904.65	4648272.63	06/07/05
P	516371.00	4648294.00	08/09/04
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A	512684.37	4649024.75	06/07/05
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P	516042.00	4649210.00	08/09/04
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A	492670.85	4652401.63	04/07/05
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A	491863.48	4652590.23	04/07/05
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A	489085.76	4653662.85	21/06/05
A	489248.22	4653696.71	21/06/05
A	515475.00	4653697.00	17/08/04
A	493851.13	4653700.81	04/07/05

Pres Lh	*Longitude*	*Latitude*	*Date*
A	510464.14	4653799.79	06/07/05
A	515924.00	4653804.00	17/08/04
A	493781.76	4653828.63	04/07/05
A	488394.00	4653876.00	11/05/05
A	490041.24	4653900.41	21/06/05
A	500120.00	4653915.00	11/05/05
A	493552.57	4653978.18	04/07/05
A	499979.00	4654032.00	11/05/05
A	488394.00	4654062.00	11/05/05
A	490053.34	4654071.93	21/06/05
A	515342.00	4654091.00	17/08/04
P	515937.00	4654115.00	17/08/04
A	497085.03	4654164.44	20/05/05
A	493334.70	4654192.76	04/07/05
A	488416.00	4654231.00	11/05/05
A	490169.35	4654240.59	21/06/05
P	511368.42	4654261.86	06/07/05
P	510789.30	4654267.73	06/07/05
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A	493601.19	4654336.57	04/07/05
A	515443.00	4654372.00	17/08/04
A	493798.37	4654420.13	04/07/05
A	488217.05	4654423.97	21/06/05
A	493749.86	4654425.17	04/07/05
A	497002.62	4654461.30	20/05/05
A	493839.39	4654486.77	04/07/05
A	493958.40	4654530.46	04/07/05
A	511421.46	4654540.52	06/07/05
P	515841.00	4654542.00	17/08/04
A	488249.00	4654567.00	11/05/05
A	493979.00	4654602.00	11/05/05
A	493974.00	4654615.00	11/05/05
A	496920.21	4654638.65	20/05/05
A	494198.00	4654641.00	11/05/05
A	490483.80	4654658.84	21/06/05
A	511777.04	4654659.81	06/07/05
A	494243.00	4654665.00	11/05/05
P	510887.06	4654670.29	06/07/05
A	515253.00	4654701.00	17/08/04
P	494338.00	4654702.00	11/05/05
A	511992.96	4654705.68	06/07/05
A	490726.12	4654728.75	08/07/05
A	500064.00	4654762.00	11/05/05
P	494460.00	4654771.00	11/05/05
P	494525.00	4654785.00	11/05/05
A	514679.00	4654809.00	17/08/04
P	494519.00	4654817.00	11/05/05
A	496800.42	4654817.89	20/05/05
P	494582.00	4654824.00	11/05/05
P	492744.91	4654827.47	08/07/05
A	512320.47	4654829.28	06/07/05
A	496853.00	4654874.00	11/05/05
A	499754.00	4654876.00	11/05/05
P	494623.00	4654881.00	11/05/05
A	512526.13	4654882.98	06/07/05
P	510469.22	4654894.03	06/07/05
P	499725.00	4654895.00	11/05/05
A	491129.41	4654915.07	08/07/05
P	494475.52	4654919.00	04/07/05
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P	510034.25	4654920.96	06/07/05
A	499773.00	4654929.00	11/05/05
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A	492430.31	4654971.44	08/07/05
A	496045.13	4654972.52	20/05/05
A	491471.52	4654973.19	08/07/05
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P	492385.67	4655002.86	08/07/05
A	492373.70	4655010.26	08/07/05
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A	494936.00	4655035.00	11/05/05
P	499816.00	4655035.00	11/05/05
A	492327.84	4655036.91	08/07/05
P	500476.00	4655052.00	11/05/05
A	500505.00	4655052.00	11/05/05
A	492283.67	4655055.84	08/07/05
A	500417.00	4655059.00	11/05/05
P	494528.00	4655060.00	11/05/05
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A	496355.00	4655116.00	11/05/05
A	513335.33	4655121.83	06/07/05
A	494762.00	4655125.00	11/05/05
A	509628.24	4655134.96	06/07/05
P	499750.00	4655138.00	11/05/05
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P	499695.00	4655146.00	11/05/05
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A	499858.00	4655148.00	11/05/05
P	499542.00	4655149.00	11/05/05
P	499620.00	4655151.00	11/05/05
A	500549.00	4655151.00	11/05/05
A	495661.00	4655155.00	11/05/05
A	491465.00	4655162.55	08/07/05
A	492111.38	4655165.65	08/07/05
A	514496.00	4655172.00	17/08/04
A	496270.00	4655175.00	11/05/05

Pres Lh	*Longitude*	*Latitude*	*Date*
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A	492980.10	4655190.11	08/07/05
P	499671.00	4655199.00	11/05/05
A	491844.49	4655210.02	08/07/05
P	499615.00	4655211.00	11/05/05
P	499592.00	4655225.00	11/05/05
P	499616.00	4655225.00	11/05/05
A	496435.00	4655228.00	11/05/05
A	496552.00	4655231.00	11/05/05
A	494554.56	4655253.01	04/07/05
A	501023.00	4655254.00	11/05/05
A	494589.71	4655257.62	04/07/05
A	493947.00	4655267.00	11/05/05
A	496411.00	4655268.00	11/05/05
A	494528.19	4655268.85	04/07/05
A	501653.00	4655272.00	11/05/05
A	494808.00	4655275.00	11/05/05
A	496609.00	4655275.00	11/05/05
A	495176.18	4655290.14	04/07/05
A	494648.95	4655290.22	04/07/05
A	496557.00	4655300.00	11/05/05
A	496688.00	4655313.00	11/05/05
A	513251.28	4655322.82	06/07/05
A	494943.00	4655329.00	11/05/05
A	509361.06	4655340.61	06/07/05
A	514068.87	4655360.58	06/07/05
A	499510.00	4655363.00	11/05/05
A	494729.08	4655363.19	04/07/05
A	493039.90	4655375.69	08/07/05
P	513923.69	4655378.32	06/07/05
A	495178.60	4655389.42	04/07/05
A	495092.24	4655395.02	04/07/05
P	513823.25	4655413.10	06/07/05
A	493311.32	4655423.29	08/07/05
A	494839.00	4655425.00	11/05/05
A	494824.82	4655432.14	04/07/05
P	514530.00	4655434.00	17/08/04
A	493401.05	4655445.01	04/07/05
A	493757.04	4655461.10	04/07/05
A	494920.95	4655466.80	04/07/05
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A	493850.00	4655477.00	11/05/05
A	494810.30	4655477.52	04/07/05
A	513607.77	4655478.58	06/07/05
A	493649.77	4655480.15	08/07/05
A	494892.00	4655485.00	11/05/05
P	514680.00	4655485.00	17/08/04
A	494629.00	4655492.00	11/05/05
A	494066.00	4655495.00	11/05/05
A	493570.63	4655502.88	04/07/05
A	496783.00	4655527.00	11/05/05
A	496308.00	4655528.00	11/05/05
A	494181.36	4655530.45	04/07/05
A	494314.00	4655542.00	11/05/05
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A	495182.12	4655569.68	04/07/05
A	500513.00	4655572.00	11/05/05
A	494430.67	4655574.05	04/07/05
A	496294.00	4655575.00	11/05/05
A	495345.03	4655585.98	04/07/05
A	495394.89	4655590.35	04/07/05
A	496309.00	4655602.00	11/05/05
A	503276.00	4655607.00	11/05/05
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A	493644.05	4655613.47	04/07/05
A	515160.00	4655636.00	17/08/04
P	513999.21	4655696.92	06/07/05
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A	515271.00	4655860.00	17/08/04
A	515077.00	4655875.00	17/08/04
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A	496997.00	4656034.00	11/05/05
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A	496706.89	4656228.37	08/07/05
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A	499103.00	4656425.00	11/05/05
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A	516426.25	4656887.77	16/06/05
P	516056.86	4656909.80	27/05/05
A	516397.30	4656925.48	16/06/05
A	508437.55	4656939.46	07/07/05
P	515674.00	4656952.00	13/09/04

Pres Lh	*Longitude*	*Latitude*	*Date*
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P	515855.64	4656970.45	27/05/05
P	515822.51	4656976.50	27/05/05
A	516328.01	4656991.66	16/06/05
P	515755.58	4657003.00	27/05/05
P	515531.36	4657005.81	27/05/05
P	516088.63	4657006.52	27/05/05
P	515546.27	4657008.16	27/05/05
P	515695.43	4657014.68	27/05/05
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P	515989.17	4657049.88	27/05/05
A	516089.19	4657053.43	27/05/05
P	515726.41	4657070.56	27/05/05
P	516026.82	4657072.63	27/05/05
A	516184.58	4657074.35	27/05/05
A	516131.86	4657076.86	27/05/05
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A	516051.93	4657089.40	27/05/05
P	515720.47	4657092.79	27/05/05
P	515992.31	4657098.04	27/05/05
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A	515668.66	4657107.02	27/05/05
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P	515729.76	4657124.06	27/05/05
P	515728.00	4657125.00	13/09/04
P	515888.69	4657130.08	27/05/05
P	515750.57	4657132.88	27/05/05
P	516022.06	4657133.64	27/05/05
P	515726.32	4657136.08	27/05/05
A	515734.54	4657141.10	27/05/05
A	515678.00	4657142.00	17/08/04
A	516192.38	4657143.93	27/05/05
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P	515941.40	4657235.37	27/05/05
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A	515726.73	4657260.54	27/05/05
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P	515938.59	4657270.62	27/05/05
P	515979.60	4657284.09	27/05/05
A	516045.91	4657284.42	27/05/05
P	515968.10	4657301.65	27/05/05
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A	515781.90	4657308.96	27/05/05
P	515904.04	4657311.38	27/05/05
A	498313.00	4657497.00	11/05/05
A	515602.00	4657516.00	13/09/04
A	502339.12	4657529.81	07/07/05
A	502323.75	4657643.93	07/07/05
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A	495881.00	4657714.00	11/05/05
A	496987.80	4657775.49	08/07/05
A	497241.93	4657787.79	08/07/05
A	502263.06	4657797.23	07/07/05
A	497083.00	4657822.00	11/05/05
A	515616.00	4657903.00	13/09/04
A	501394.40	4657920.91	07/07/05
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A	500885.32	4658083.12	07/07/05
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A	502338.16	4658180.15	07/07/05
A	502520.50	4658248.81	07/07/05
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A	502688.20	4658336.58	07/07/05
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A	502757.95	4658374.57	07/07/05
A	503301.27	4658402.51	07/07/05
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A	505900.06	4658420.53	07/07/05
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A	500005.34	4658691.89	08/07/05
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A	504755.18	4658707.28	07/07/05
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A	504235.07	4658855.55	07/07/05
A	499707.88	4658869.30	08/07/05

Pres Lh	Longitude	Latitude	Date
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A	508570.86	4658990.03	07/07/05
A	497672.00	4659034.84	08/07/05
A	499437.94	4659036.49	08/07/05
A	499384.46	4659171.32	08/07/05
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A	508814.32	4659266.73	07/07/05
P	507975.09	4659283.02	07/07/05
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A	498002.16	4659438.43	08/07/05
A	507664.62	4659556.41	07/07/05
A	514853.00	4659580.00	13/09/04
A	509078.86	4659696.65	07/07/05
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A	514689.00	4660266.00	13/09/04
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A	507246.79	4660755.47	07/07/05
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A	513717.00	4661223.00	13/09/04
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P	512597.00	4661430.00	03/05/05
P	512558.00	4661446.00	03/05/05
P	513306.00	4661505.00	13/09/04
P	512648.78	4661529.54	01/06/05
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P	511309.00	4661562.00	03/05/05
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P	512889.40	4661653.55	01/06/05
P	514044.00	4661662.00	03/05/05
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P	511125.90	4661825.45	07/07/05
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P	514001.00	4661915.00	13/09/04
P	512513.58	4661950.91	07/07/05
P	513794.97	4662008.48	07/07/05
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P	512578.42	4662326.05	07/07/05
A	507011.57	4662369.74	07/07/05
P	513152.21	4662411.29	07/07/05
P	514181.00	4662454.00	13/09/04
P	513736.00	4662473.00	13/09/04
P	512939.00	4662524.00	13/09/04
P	512669.08	4662603.37	07/07/05
P	514173.00	4662683.00	13/09/04
A	506823.74	4662758.89	07/07/05
A	506758.52	4663027.94	07/07/05
P	511352.00	4663054.00	13/09/04
A	506631.18	4663441.73	07/07/05
P	510361.00	4663728.00	13/09/04
A	506625.87	4663863.90	07/07/05
P	509851.00	4664144.00	13/09/04
P	510125.00	4664171.00	13/09/04
A	506677.58	4664245.01	07/07/05
P	510057.00	4664413.00	13/09/04
A	506590.20	4664417.95	07/07/05
A	508592.00	4664528.00	13/09/04
A	506432.04	4664648.05	07/07/05
P	506308.88	4664679.19	07/07/05
A	509263.00	4664711.00	13/09/04
A	506253.63	4664724.26	07/07/05
A	508410.00	4664869.00	13/09/04
A	508658.00	4664875.00	13/09/04
A	509315.00	4664916.00	13/09/04
A	506205.15	4664918.17	07/07/05
A	509315.00	4665004.00	13/09/04
A	506061.42	4665243.94	07/07/05
A	508429.00	4665250.00	20/09/04
P	509604.00	4665309.00	07/09/04
P	509755.00	4665484.00	13/09/04
A	505973.67	4665551.13	07/07/05
P	509603.00	4665567.00	13/09/04
P	509481.00	4665772.00	07/09/04
A	496448.51	4665968.32	05/07/05
P	509705.00	4665969.00	07/09/04
P	509601.00	4666039.00	13/09/04
A	497188.41	4666039.52	05/07/05
A	496836.28	4666040.52	05/07/05
A	505927.54	4666073.62	07/07/05
A	508198.00	4666076.00	20/09/04
A	496041.05	4666079.98	05/07/05
A	495595.85	4666141.13	05/07/05

Pres Lh	*Longitude*	*Latitude*	*Date*
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A	495357.06	4666181.36	05/07/05
A	505828.29	4666252.54	07/07/05
A	494863.40	4666267.53	05/07/05
A	494565.96	4666288.49	05/07/05
A	497972.10	4666467.91	05/07/05
A	509255.00	4666477.00	07/09/04
A	493933.13	4666550.78	05/07/05
A	505831.60	4666658.26	07/07/05
A	498437.56	4666706.61	05/07/05
A	493721.85	4666750.47	05/07/05
A	498682.30	4666887.02	05/07/05
A	505711.15	4667046.07	07/07/05
P	505926.27	4667112.55	07/07/05
A	505980.97	4667138.19	07/07/05
A	505917.96	4667197.29	07/07/05
A	493598.43	4667208.03	05/07/05
A	498854.72	4667220.49	05/07/05
A	507743.00	4667246.00	20/09/04
A	499089.35	4667295.14	05/07/05
A	492706.68	4667416.24	05/07/05
A	493169.24	4667422.37	05/07/05
A	493485.63	4667424.20	05/07/05
A	506049.14	4667496.01	07/07/05
A	507615.00	4667592.00	20/09/04
A	499189.52	4667693.83	05/07/05
A	506087.49	4667732.42	07/07/05
P	508999.00	4667811.00	07/09/04
A	506252.08	4667924.29	07/07/05
A	499322.85	4668072.47	05/07/05
A	506089.30	4668247.69	07/07/05
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A	501334.42	4668715.54	05/07/05
A	500991.47	4668722.87	05/07/05
A	509250.00	4668771.00	07/09/04
A	499359.21	4668791.25	05/07/05
A	506557.00	4668817.00	20/09/04
A	501711.13	4668849.74	05/07/05
A	506019.02	4668860.79	07/07/05
A	502123.82	4668904.10	05/07/05
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A	502475.11	4669004.08	05/07/05
A	499237.72	4669084.41	05/07/05
A	507823.00	4669135.00	07/09/04
A	500113.57	4669197.83	05/07/05
A	502842.59	4669198.27	05/07/05
A	508052.00	4669252.00	07/09/04
A	503846.82	4669258.32	05/07/05
A	503370.78	4669282.05	05/07/05
A	503175.93	4669314.82	05/07/05
A	500005.43	4669323.14	05/07/05
A	499412.95	4669336.58	05/07/05
A	503489.15	4669404.29	05/07/05
A	504052.45	4669484.28	05/07/05
A	499908.93	4669626.12	05/07/05
A	504362.72	4669639.54	05/07/05
A	509160.00	4669689.00	07/09/04
A	508595.00	4669760.00	07/09/04
P	507755.00	4669892.00	07/09/04
A	505071.25	4669911.90	05/07/05
P	508846.00	4670165.00	07/09/04
A	505741.19	4670175.75	05/07/05
P	507803.00	4670441.00	07/09/04
A	506335.03	4670519.63	05/07/05
P	507658.00	4670603.00	07/09/04
A	506580.38	4670606.66	05/07/05
A	506762.20	4670620.59	05/07/05
A	507968.00	4670809.00	07/09/04
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A	509073.00	4670927.00	07/09/04
A	506791.00	4671240.00	07/09/04
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A	508810.00	4672310.00	07/09/04
A	509129.00	4672555.00	07/09/04
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A	508327.00	4673009.00	20/09/04
A	507221.00	4673564.00	20/09/04
A	507663.00	4673610.00	20/09/04
A	507720.00	4674898.00	20/09/04
A	507559.00	4675536.00	20/09/04
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A	518420.00	4677098.00	20/09/04
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P	508722.00	4677400.00	20/09/04
P	510240.00	4677452.00	20/09/04
P	516386.00	4677491.00	20/09/04
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P	518674.00	4677552.00	20/09/04
P	516639.00	4677692.00	20/09/04
A	511097.00	4677798.00	20/09/04
A	519268.00	4677813.00	20/09/04
P	518680.00	4677855.00	20/09/04
P	519072.00	4677997.00	20/09/04
A	517431.00	4678039.00	20/09/04
A	518706.00	4678172.00	20/09/04

Pres Lh	*Longitude*	*Latitude*	*Date*
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P	507399.00	4678261.00	20/09/04
A	518596.00	4678311.00	20/09/04
A	516461.00	4678322.00	20/09/04
P	506143.27	4678393.50	05/07/05
P	515077.00	4678408.00	20/09/04
A	505307.91	4678432.54	05/07/05
A	505742.78	4678458.76	05/07/05
A	510143.00	4678478.00	20/09/04
A	518286.00	4678516.00	20/09/04
P	506643.00	4678604.00	20/09/04
A	505645.44	4678605.71	05/07/05
A	505134.66	4678626.50	05/07/05
A	505407.25	4678675.41	05/07/05
A	509729.00	4678679.00	20/09/04
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A	504948.14	4678838.15	05/07/05
A	514882.00	4678850.00	20/09/04
A	505661.67	4678859.57	05/07/05
A	515823.00	4678861.00	20/09/04
A	515661.00	4678985.00	20/09/04
A	504796.58	4678987.37	05/07/05
A	515534.00	4679023.00	20/09/04
A	504421.03	4679143.17	05/07/05
A	504207.82	4679221.52	05/07/05
A	499889.75	4679268.98	05/07/05
A	499735.48	4679273.65	05/07/05
A	511998.00	4679345.00	20/09/04
P	515458.00	4679347.00	20/09/04
A	500176.97	4679387.64	05/07/05
A	503905.17	4679423.88	05/07/05
A	501769.07	4679457.47	05/07/05
A	499702.67	4679472.89	05/07/05
A	501409.89	4679501.09	05/07/05
A	503021.97	4679534.44	05/07/05
A	502748.67	4679535.98	05/07/05
A	501194.59	4679561.03	05/07/05
A	503548.42	4679563.44	05/07/05
A	501882.18	4679601.60	05/07/05
A	500369.57	4679602.40	05/07/05
A	503288.75	4679605.85	05/07/05
A	500637.40	4679669.65	05/07/05
A	499717.88	4679689.74	05/07/05
A	502371.28	4679694.70	05/07/05
A	502451.34	4679826.12	05/07/05
A	513729.00	4679831.00	20/09/04
P	512631.00	4679832.00	20/09/04
P	512891.00	4680003.00	11/08/04
A	515183.00	4680032.00	20/09/04
A	522490.00	4682128.00	11/08/04
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A	523259.00	4682660.00	11/08/04
A	517071.00	4682694.00	11/08/04
A	523461.00	4682934.00	11/08/04
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A	523857.00	4683314.00	11/08/04
A	517958.00	4684518.00	23/09/04
A	523847.00	4684961.00	11/08/04
A	526026.00	4685419.00	11/08/04
A	525053.51	4685430.72	21/06/05
A	525146.00	4685470.46	21/06/05
A	525148.62	4685482.18	21/06/05
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A	525151.05	4685578.79	21/06/05
A	525051.38	4685588.05	21/06/05
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A	524385.11	4685597.46	21/06/05
A	525002.45	4685600.42	21/06/05
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A	524673.32	4685642.98	21/06/05
A	524655.56	4685649.57	21/06/05
A	524660.37	4685650.92	21/06/05
A	524648.15	4685657.41	21/06/05
A	524636.09	4685667.32	21/06/05
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A	524647.58	4685671.32	21/06/05
P	524630.98	4685685.13	21/06/05
A	524618.42	4685689.65	21/06/05
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P	524572.24	4685711.45	21/06/05
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P	524625.61	4685752.48	21/06/05
P	524379.12	4685755.81	21/06/05
P	524623.97	4685758.61	21/06/05
A	524366.97	4685770.22	21/06/05
P	524627.62	4685774.16	21/06/05
A	524385.87	4685774.49	21/06/05
P	524367.40	4685783.89	21/06/05
A	524344.19	4685802.35	21/06/05
P	524631.01	4685810.15	21/06/05
A	524327.10	4685815.54	21/06/05

Pres Lh	Longitude	Latitude	Date
P	524618.73	4685816.88	21/06/05
P	524611.74	4685823.87	21/06/05
A	524307.48	4685824.64	21/06/05
P	524642.36	4685826.61	21/06/05
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P	524618.46	4685848.74	21/06/05
P	524637.07	4685850.73	21/06/05
P	524645.83	4685861.76	21/06/05
P	524600.04	4685862.96	21/06/05
P	524668.25	4685865.21	21/06/05
P	524617.63	4685885.76	21/06/05
A	524728.23	4685897.75	21/06/05
P	524628.18	4685904.84	21/06/05
P	524597.63	4685907.97	21/06/05
A	524733.80	4685908.62	21/06/05
A	524723.16	4685913.39	21/06/05
P	524670.67	4685923.76	21/06/05
A	524740.71	4685924.18	21/06/05
A	524734.66	4685929.99	21/06/05
P	524690.68	4685930.55	21/06/05
P	524558.56	4685937.52	21/06/05
P	524547.10	4685943.65	21/06/05
P	524535.07	4685953.14	21/06/05
A	524750.80	4685954.53	21/06/05
A	524756.20	4685966.89	21/06/05
P	524517.34	4685971.76	21/06/05
A	524748.06	4685980.07	21/06/05
A	524765.05	4685989.29	21/06/05
A	524758.91	4685989.86	21/06/05
A	524769.28	4686005.86	21/06/05
A	524738.89	4686029.60	21/06/05
A	524782.08	4686038.40	21/06/05
P	524738.51	4686041.92	21/06/05
P	524802.58	4686042.99	21/06/05
P	524818.02	4686058.82	21/06/05
A	524836.79	4686072.74	21/06/05

Pres Lh	Longitude	Latitude	Date
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A	524859.87	4686091.54	21/06/05
A	524872.14	4686106.12	21/06/05
A	524881.20	4686124.61	21/06/05
P	524904.72	4686142.33	21/06/05
A	525000.54	4686143.61	21/06/05
A	524933.49	4686147.53	21/06/05
A	517005.00	4686256.00	23/09/04
A	516183.00	4686361.00	23/09/04
A	516112.00	4686830.00	23/09/04
P	515899.00	4686938.00	23/09/04
A	506643.16	4686983.40	12/07/05
P	515978.00	4687057.00	23/09/04
A	506368.46	4687143.33	12/07/05
A	507012.44	4687204.10	12/07/05
A	513963.00	4687292.00	23/09/04
A	516885.00	4687395.00	23/09/04
P	515633.00	4687415.00	23/09/04
A	515499.00	4687552.00	23/09/04
A	507309.98	4687633.92	12/07/05
P	505487.82	4687678.21	12/07/05
A	514972.00	4687764.00	23/09/04
A	515387.00	4687881.00	23/09/04
P	507521.35	4687883.88	12/07/05
A	515174.00	4687943.00	23/09/04
A	516828.00	4687960.00	23/09/04
P	505113.83	4687982.81	12/07/05
A	516738.00	4688003.00	23/09/04
A	504916.94	4688178.20	12/07/05
A	517155.00	4688251.00	23/09/04
P	504547.24	4688353.42	12/07/05
A	508038.44	4688502.49	12/07/05
A	503994.30	4688604.67	12/07/05
A	510178.00	4688615.00	22/09/04
A	514575.00	4688740.00	23/09/04
A	510772.00	4688753.00	22/09/04

Pres Lh	Longitude	Latitude	Date
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A	503558.28	4688942.81	12/07/05
A	515017.00	4688986.00	23/09/04
A	508953.05	4689088.21	12/07/05
A	509015.00	4689173.00	22/09/04
A	514396.00	4689173.00	23/09/04
A	511627.00	4689181.00	22/09/04
A	514115.00	4689247.00	23/09/04
A	503173.76	4689304.25	12/07/05
P	514128.00	4689317.00	23/09/04
A	513811.00	4689349.00	23/09/04
A	513786.00	4689427.00	23/09/04
A	513653.00	4689577.00	23/09/04
A	492203.15	4689607.41	12/07/05
A	513436.00	4689633.00	23/09/04
A	502907.89	4689753.36	12/07/05
A	513324.00	4689848.00	23/09/04
A	512876.00	4689862.00	23/09/04
A	511240.00	4689961.00	22/09/04
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P	512078.00	4690011.00	22/09/04
A	512978.00	4690050.00	23/09/04
P	513367.00	4690065.00	23/09/04
A	492334.84	4690091.69	12/07/05
A	497474.98	4690112.21	12/07/05
A	513164.00	4690130.00	23/09/04
A	512768.00	4690209.00	23/09/04
A	502572.53	4690261.07	12/07/05
A	492458.17	4690288.31	12/07/05
A	498043.42	4690366.26	12/07/05
A	496775.53	4690443.96	12/07/05
A	513512.00	4690569.00	23/09/04
A	502285.43	4690620.86	12/07/05
P	512436.00	4690631.00	22/09/04
A	492594.43	4690642.84	12/07/05
P	512408.00	4690701.00	22/09/04

Pres Lh	*Longitude*	*Latitude*	*Date*
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A	498537.77	4690810.44	12/07/05
A	492834.47	4690894.04	12/07/05
A	513055.00	4690912.00	23/09/04
A	493224.45	4691019.93	12/07/05
A	494522.94	4691082.75	12/07/05
A	512747.00	4691122.00	22/09/04
A	498672.57	4691161.03	12/07/05
A	495716.88	4691216.35	12/07/05
A	493669.40	4691258.90	12/07/05
A	502396.22	4691359.16	12/07/05
A	494101.42	4691408.65	12/07/05
A	501696.87	4691490.15	12/07/05
A	494984.73	4691502.19	12/07/05
A	501460.28	4691691.23	12/07/05
A	498802.24	4691704.59	12/07/05
P	512855.00	4691793.00	22/09/04
A	502185.43	4691803.48	12/07/05
A	501080.77	4691965.90	12/07/05
P	512699.00	4692013.00	22/09/04
A	498918.80	4692065.93	12/07/05
A	498955.11	4692114.74	12/07/05
A	498795.71	4692320.78	12/07/05
A	499541.55	4692411.26	12/07/05
P	512816.00	4692457.00	22/09/04
A	500685.20	4692458.61	12/07/05
A	498789.77	4692610.18	12/07/05
P	512655.00	4692612.00	22/09/04
A	500363.74	4692782.88	12/07/05
A	499800.64	4692872.47	12/07/05
P	513195.00	4692878.00	22/09/04
P	512658.00	4692889.00	22/09/04
A	498596.59	4692905.03	12/07/05
P	512832.00	4693010.00	22/09/04
P	513019.00	4693061.00	22/09/04
P	513146.00	4693085.00	22/09/04
A	500132.55	4693113.75	12/07/05
A	498512.63	4693257.21	12/07/05
A	500086.24	4693400.80	12/07/05
A	512571.00	4693428.00	22/09/04
A	498266.61	4693509.40	12/07/05
A	499270.90	4693538.17	12/07/05
A	499094.00	4693661.68	12/07/05
A	500018.61	4693688.11	12/07/05
A	498762.92	4693716.43	12/07/05
A	499311.41	4693719.20	12/07/05
A	498447.75	4693719.22	12/07/05
A	499960.82	4693976.72	12/07/05
A	499165.51	4694036.41	12/07/05
A	499839.81	4694196.20	12/07/05
A	512608.00	4694241.00	22/09/04
A	499296.23	4694327.25	12/07/05
A	499362.02	4694428.70	12/07/05
A	499255.33	4694439.96	12/07/05
A	499255.53	4694440.61	12/07/05
A	499421.56	4694468.36	12/07/05
A	499640.77	4694548.07	12/07/05
A	512265.00	4694618.00	22/09/04
A	511789.00	4694624.00	22/09/04
A	499442.93	4694626.37	12/07/05
A	512964.00	4694865.00	22/09/04
A	513060.00	4695384.00	22/09/04
A	513476.00	4695701.00	22/09/04
A	513904.00	4696984.00	22/09/04
A	513446.00	4697131.00	22/09/04
A	512772.00	4697230.00	22/09/04
A	513451.00	4697385.00	22/09/04

A fora, al costat del niu, la Formiga Piga va veure que s'havia format una muntanya negra. Una muntanya grandiosa que gairebé arribava fins al cel. Com que era tan a prop, va decidir de pujar-hi a veure si estava feta de pedra dura, d'argila o de sorra.

Quan només havia començat la pujada, la muntanya es va moure. Al començament la Formiga Piga gairebé no ho va notar. Però com que la muntanya s'enlairava, com si volés, i després tornava a terra, la Formiga Piga es va adonar que de tant en tant les fileres de formigues eren més petites i més llunyanes i per això va trobar que la muntanya negra caminava com un animal del bosc.

I així, amagada i quieta dins d'un foradet de la muntanya perquè les sacsejades no la fessin caure, la Formiga Piga va veure com s'allunyava del bosc i entrava en una mena de cova tan negra com la muntanya.

Un cop dins la cova, la muntanya es va quedar quieta. Però de sobte va sentir-se un soroll molt estrany, com si tota la cova trontollés tot i que la muntanya no es movia.

I més endavant van començar a sentir-se veus i riures i cançons i la Formiga Piga, una mica espantada, va començar a preocupar-se per si no podia tornar al niu. I a preocupar-se a quina mena de muntanya desconeguda s'havia enfilat.

El cas és que a poc a poc la Formiga Piga es va adonar que havia pujat a la sabata d'un home que visitava el bosc i que després havia tornat cap a la ciutat en un cotxe.

I ara la Formiga Piga es trobava molt lluny del seu cau i no podia tornar-hi. I a quin niu la voldrien si no feia la seva olor? Segurament que no podria tornar a veure la seva reina i les seves companyes fins que a aquell senyor li vingués bé de visitar un altre cop el bosc. I qui sabia quant de temps podia passar fins que aquella sabata tornés a trepitjar el prat on s'obria el forat del seu niu?

La Formiga Piga tremolava en pensar que el senyor potser no tindria ganes de tornar-hi mai més. I potser, si hi tornava, no portaria les mateixes sabates!

(...)

I així, al cap del temps i de mots esforços, va arribar a entendre que aquell senyor era un periodista que estava a punt de fer la volta al món!

Res de tornar al niu. En lloc de tornar a casa, la Formiga Piga hauria de fer ... la volta al món!

De primer la Formiga Piga es va posar trista perquè veia impossible tornar a aviat al niu, però després va pensar que podia aprofitar l'oportunitat per conèixer tota la terra i veure com era el món fins i tot més enllà de l'horitzó.

I va decidir portar d'equipatge una llibreta petita per anar-hi escrivint i dibuixant les coses més importants que trobés en el viatge, de manera que en tornar al niu podria explicar a tot el formiguer com era el món i les persones i els animals que l'habitaven.

Com deia la Formiga Vella, "el saber no fa cap nosa".

E. Teixidor.
(*La volta al món de la Formiga Piga*)