

Predicting the global spread of an invasive pollinator, the bumblebee *Bombus terrestris*.

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31

32 **Abstract**

33 The global trade in commercial bumblebees for crop pollination, particularly of the
34 common European species *Bombus terrestris*, has led to a number of deliberate
35 introductions and accidental escapes of this species far from its native range. This poses
36 environmental risks, particularly via the accidental co-introduction of non-native parasites
37 which can have devastating impacts on native bees. Here we use climatic niche modelling
38 (Maxent) based on the well-characterised European distribution of *B. terrestris* to predict
39 areas of the globe at risk from invasion by this species. The model is validated by
40 comparison with the known distribution of invasive *B. terrestris* (in Japan, New Zealand,
41 Tasmania, South America, and possibly South Korea); all known invasions are in areas
42 predicted by the model to be suitable. Other areas which the model predicts to be at risk of
43 invasion include southern South Africa, southern Australia, parts of North America, and
44 substantial areas of China. The invasion of South America by *B. terrestris* is on-going, and
45 resulting in the southward retreat of the native *B. dahlbomii*, probably mediated by a non-
46 native parasite carried by *B. terrestris*. Our model predicts that *B. terrestris* will continue to
47 invade southwards to the tip of South America, such that *B. dahlbomii* is in imminent
48 danger of extinction.

49 **Introduction**

50

51 There are approximately 250 known species of bumblebees (genus *Bombus*), naturally
52 distributed throughout the Northern Hemisphere and South America (Williams 1994). In
53 temperate zones they are among the most important wild pollinators, delivering pollination
54 to a range of arable and horticultural crops and innumerable wildflower species (Goulson
55 2010). Their aptitude for buzz pollination, a skill not shared by honeybees, led to the
56 commercialization of bumblebee rearing to provide colonies for tomato pollination in the
57 late 1980s (Velthuis & van Doorn 2006). Bumblebee rearing rapidly became a global
58 business; colonies are used mainly for tomato pollination, but they are also used for a range
59 of other glasshouse and field crops including peppers, aubergines, various curcubits and
60 soft fruits (Goulson 2003). The trade started with a common European species, *Bombus*
61 *terrestris*, and this species still dominates global trade although other local species are
62 reared in some regions. Estimates from 2004 suggest that the global bumblebee trade
63 consisted of approximately 930,000 colonies of *B. terrestris*, approximately 55,000
64 colonies of the North American *B. impatiens*, and a few thousand colonies of the Eurasian
65 *B. lucorum*, east Asian *B. ignitus*, and North American *B. occidentalis* (Velthuis & van
66 Doorn 2006). More recent estimates are not available but the number of colonies used is
67 likely to be considerably higher, with *B. terrestris* now exported to at least 60 countries
68 worldwide (Goulson 2010).

69 This widespread trade has been accompanied by various deliberate releases and
70 accidental escapes, such that *Bombus terrestris* has now become established in several
71 regions of the globe to which it is not native. In fact anthropogenic redistribution of
72 bumblebees began in the late 1800s, long before the commercial trade developed, when
73 four species of bumblebee, including *B. terrestris*, were introduced to New Zealand where
74 they flourish to this day (Goulson & Hanley 2004). Following the commencement of
75 commercial rearing, *B. terrestris* became established in the wild in Japan in the early 1990s
76 following escapes from glasshouses (Goka 1998). In 1992, *B. terrestris* stock from New
77 Zealand arrived in Hobart, Tasmania, their means of transport unknown, and they have
78 since spread to occupy the entire island (Semmens 1996; Buttermore 1997). In 1998, *B.*
79 *terrestris* were deliberately introduced to Chile, from whence they crossed the Andes to

80 Argentina in 2006 (Torretta *et al.* 2006). Most recently, anecdotal evidence suggests that *B.*
81 *terrestris* had escaped from glasshouses and established in the wild in South Korea by
82 2002, following the routine importation of colonies from 1994 onwards (Yoon *et al.* 2009).

83 The on-going introduction and spread of *B. terrestris* is of particular concern
84 because there is clear evidence for substantial negative impacts upon native flora and fauna.
85 In New Zealand and Tasmania, pollination by *B. terrestris* contributes substantially to seed
86 set of major environmental weeds, many of which are native to Europe and co-evolved with
87 bumblebee pollinators that do not naturally occur in the Antipodes (Hanley & Goulson
88 2003; Goulson & Rotheray 2012). In Japan, there is evidence for competition with native
89 bumblebees for nesting holes, and also inter-specific mating between *B. terrestris* and the
90 native *B. hypocrita* which effectively sterilizes the *B. hypocrita* queens since no viable
91 offspring are produced (Inoue *et al.* 2008; Kanbe *et al.* 2008). However, the biggest
92 concerns with the spread of *Bombus terrestris* relate to the accidental transportation of bee
93 parasites and pathogens, which have the potential to inflict devastating impacts on naïve
94 native bee species.

95 We have a very poor understanding of the ecology, geographic distribution and host
96 range of most bee parasites and diseases. Until very recently almost all research focussed
97 on honeybees, but it is now clear that honeybees, bumblebees and other pollinator species
98 each harbour a diverse and overlapping range of viral, bacterial, fungal, protozoan and
99 arthropod parasites. Bumblebee colonies sold for commercial use have been found to
100 commonly contain various parasites, including species which infect honeybees (Colla *et al.*
101 2006; Otterstatter & Thomson 2007; Manson *et al.* 2010; Singh *et al.* 2010; Meeus *et al.*
102 2011; Murray *et al.* 2013), so it is likely that the global trade is resulting in a wholesale
103 redistribution of bee parasites. European strains of the tracheal mite *Locustacarus buchneri*
104 now infest wild Japanese bumblebees (Goka *et al.* 2006). Dramatic declines in abundance
105 and range of several once-common North American bumblebee species have been linked to
106 the accidental introduction of a virulent strain of the microsporidian *Nosema bombi* from
107 Europe, although definitive evidence for this link is lacking (Grixti *et al.* 2009; Cameron *et al.*
108 2011). In South America, the native *B. dahlbomii* has disappeared from all areas invaded
109 by the rapidly spreading *B. terrestris*, and may face imminent extinction if *B. terrestris*
110 spreads to encompass all of its range (Arbetman *et al.* 2012). The *B. terrestris* are infected

111 at high prevalence with the neogregarine *Apicystis bombi*, a parasite not previously known
112 from South America, and this has been suggested to be the cause of the decline in *B.*
113 *dahlbomii* (Plischuk et al 2011; Arbetman et al. 2012).

114 Given the major impacts of *B. terrestris* outside its native range, there is an urgent
115 need to establish the further potential for spread of this species, to highlight regions where
116 it is likely to be able to persist in the wild, and to predict the likely extent of on-going
117 invasions. The only previous attempt to do so used habitat niche-based models to predict
118 the potential distribution of this species in Hokkaido, Japan, concluding that distribution
119 may be negatively influenced by large areas of woodland (Kadoya et al. 2009). Here, we
120 use climatic niche modelling, based on the well characterised natural distribution of *B.*
121 *terrestris* in Europe, to predict where else in the globe has climatic conditions suitable for
122 the survival of this species. Predictions are validated by comparisons with the extent of
123 known invasions, and areas where *B. terrestris* has not yet invaded but which could provide
124 suitable conditions are highlighted.

125

126 **Methods**

127 Distribution data for *B. terrestris* in Europe were obtained from the STEP project (Status
128 and Trends of European Pollinators), and included 25,085 records from Europe, North
129 Africa (Morocco, Algeria, Tunisia, Libya) and the Middle East (Jordan, Iran,
130 Turkmenistan, Uzbekistan, Kazakhstan) (Rasmont & Iserbyt, 2012). Maximum Entropy
131 Species Distribution Modelling software (Maxent Version 3.3.3, Phillips et al. 2006) was
132 used to predict the global potential for invasion of *B. terrestris*. Maxent is a machine-
133 learning process based on a statistical mechanics approach that uses presence-only data to
134 predict habitat-suitability across the studied area.

135 Maxent estimated the potential for invasion by finding the Maxent distribution
136 given the constraint that the expected value for each variable closely matches the empirical
137 average of the occurrence data (Phillips & Dudík 2008). For this model calculation, we
138 used presence-only data, at a 1 degree resolution. Hence, a 1 degree resolution set of global
139 environmental variables were selected as predictors. The 6 selected environmental variables
140 (mean annual temperature (°C), mean annual minimum temperature (C°), mean annual
141 maximum temperature (C°), mean annual precipitation (mm), mean annual diurnal

142 temperature range (°C), and frost days) were obtained from CRU (Climatic Research Unit,
143 2012. These climatic variables were selected based on their likely relevance to bumblebees
144 based on our understanding of their thermoregulatory abilities and life-history (Heinrich,
145 1979; Goulson 2010; Iserbyt & Rasmont, 2012).

146 To check which environmental variables were the most important for model
147 building, a jack-knife analysis of the gain was produced to analyze how well each
148 environmental variable distinguished localities where the species naturally occurs from the
149 rest of the world.

150 Model predictions were compared to known locations of invasion by *B. terrestris*
151 outside their native range (South America, Japan, Tasmania, New Zealand). To test the
152 sensitivity of the Maxent results, they were compared to field records of the distribution of
153 *B. terrestris* in New Zealand (a long-established distribution) and Argentina (where
154 invasion is ongoing). For New Zealand, distribution data were obtained from Goulson and
155 Hanley (2004), based on one man-hour searches of 74 sites in South Island carried out in
156 2003. For Argentina, records were obtained from ½ man-hour searches of 54 sites within
157 and beyond the currently advancing distribution of *B. terrestris*, in a survey which
158 attempted to establish the extent of the northerly and easterly spread of the species, carried
159 out by D.G. and J.J.S. in January 2012.

160

161 **Results**

162

163 Determination of most relevant climatic variables for MAXENT

164 Maxent jack-knife analysis (Figure 1) showed that the most important variable for the
165 Maxent distribution of *B. terrestris* was mean maximum temperature (TMX) which had the
166 highest contribution to the model. The probability of occupancy is predicted to be low for
167 areas where TMX exceeds ~25°C. The three temperature variables showed the highest gain
168 when used in isolation, showing that temperature is the most useful single predictor. The
169 probability of occupancy was markedly higher in regions with a mean annual temperature
170 between ~0 and 18°C, and a mean annual minimum temperature between -5 and 15°C. Sites
171 were predicted to have low probability of occupancy if there were more than 200 frost days
172 per year, and if the mean annual diurnal temperature range is less than 6°C. Mean annual

173 precipitation (PRE) was the least correlated variable, since it showed only a slight decrease
174 in gain when omitted in comparison to the other variables. Sites were predicted to have a
175 low probability of occupancy of there was less than 200mm of rain per year.

176 The model predicts the climatic niche of *B. terrestris* outside of its natural range of
177 distribution (Figure 2). This can be interpreted as the potential for invasion of *B. terrestris*,
178 defined as the probability that areas outside of its natural range are suitable for the species
179 to survive. All known invasions of *B. terrestris* outside of its native range are in areas
180 which the model predicts to be suitable; New Zealand, Tasmania, Japan and southern South
181 America. South Korea is also predicted to be suitable, although the invasion status in this
182 country is unclear (Yoon et al 2009). No invasions have been recorded in areas that the
183 model predicts to be unsuitable (probability of suitability for occupation < 0.001; Eastman,
184 2009).

185 For New Zealand, all regions were predicted to be suitable for occupation by *B.*
186 *terrestris* (Maxent probabilities ranged from 0.097 to 0.669). The species was detected in
187 67 of the 74 sites surveyed, and is regarded as ubiquitous on South Island (Goulson &
188 Hanley 2004). The locations in which *B. terrestris* were found spanned a range of Maxent
189 probabilities from 0.100 to 0.506.

190 In Argentina, of the 54 sites surveyed in January 2012, *B. terrestris* were detected at
191 ten, and the survey revealed that the invasion front has advanced approximately 700 km
192 northwards in Argentina from the location near Bariloche where the species first crossed
193 the Andres in 2006 (Torretta *et al.* 2006), a rate of spread exceeding 100 km per year
194 (Figure 3). Maxent probabilities for occupied sites ranged from 0.011 to 0.128. Unoccupied
195 sites ranged from those with very low probability (0.002) up to sites which are predicted to
196 be highly suitable (0.461). However, the most suitable sites according to the model were on
197 the Atlantic coast south of Buenos Aires, far from the site of invasion. Other sites of
198 relatively high predicted suitability were to the north of the currently northwards-advancing
199 population front, and are currently occupied by the native *Bombus opifex* (D.G. and J.J.S.,
200 unpublished data).

201

202 Potential for further invasions

203 The model identified a number of areas that are currently unoccupied as being climatically
204 suitable for *B. terrestris*; the southern mainland of Australia (Figure 2), substantial parts of
205 China and Korea, the Himalayas, the southern tip of Africa, parts of eastern and north
206 western North America (Figure 2), the southern tip of South America and parts of the east
207 coast of Argentina (Figure 3).

208 Predictions as to the likely final extent of the ongoing invasion of South America
209 are of particular interest. The model predicts that the climate is suitable to the tip of Tierra
210 del Fuego (Figure 3), but that *B. terrestris* may be approaching the northern limit of
211 suitable climatic niche space. To the east, the coastal area south of Buenos Aires and
212 stretching northwards into Uruguay is predicted to be suitable, but is separated from the
213 areas currently being invaded by *B. terrestris* to the south and west of Argentina by a
214 substantial barrier of arid semi-desert which the model identified as unsuitable.

215

216 **Discussion**

217 The model's predictions agree well with the known instances of establishment of *B.*
218 *terrestris* outside of its native range, suggesting that the predictions are valid. It should be
219 noted that our data on the European distribution of *B. terrestris* include a number of named
220 subspecies / races which may differ in their climatic tolerances, so the potential for spread
221 may vary according to their origins (Rasmont et al., 2008). After the initial transportation of
222 the ssp. *B. terrestris audax* from UK to New Zealand (and hence to Tasmania), the
223 subspecies that are presently the most exported from Europe are ssp. *dalmatinus*, ssp.
224 *terrestris* s.s. and likely their hybrids. These subspecies have the largest distribution areas,
225 from the Mediterranean to near the Arctic Circle, and occur in most European biomes
226 (including mountains, steppes, Mediterranean matorrals, deciduous forest, boreal taiga and
227 most anthropogenic habitats). Their ability to undergo several generations per year, even in
228 winter (Rasmont et al. 2008), presumably facilitates survival across a broad range of
229 climates. However, our predictions here are based on the entire native range of all
230 subspecies combined.

231 The model's predictions allow us to highlight a number of geographic regions
232 where importation of *B. terrestris* would run a high risk of escape and establishment, and
233 thus where it is particularly important to prevent such trade. Because of their value as

234 commercial pollinators, applications have previously been lodged by horticulturalists for
235 the deliberate release of *B. terrestris* in mainland Australia, with the most recent application
236 being rejected in 2008 (Goulson 2010). Invasion of *B. terrestris* is classified as a “*Key*
237 *Threatening Process*” by the New South Wales Department of Environment (Adams
238 2004). Our analysis strongly suggests that such an introduction would run a high risk of the
239 bees establishing and spreading in southern parts of mainland Australia, with unknown
240 consequences for Australia’s unique plant and pollinator communities.

241 The extent of the global trade in bumblebees is impossible to establish, in part
242 because the companies that rear the nests regard information on the markets they supply to
243 be commercially sensitive. As long ago as 1998, Dafni listed countries which import *B.*
244 *terrestris* to include Japan, China, Korea, Chile, Uruguay, Argentina and South Africa, but
245 it seems certain that there are many more. Of these seven countries, three have already been
246 invaded, but our model predictions suggest that South Africa, China and Korea are also at
247 high risk. In South Korea, many thousands of *B. terrestris* colonies are currently used,
248 although the native *B. ignitus* are also commercially available (Lee et al. 2010).

249 Given the environmental risks associated with importation and use of non-native
250 bumblebees, this practice should be discontinued. In Asia there are native species that have
251 already been commercialized, and it seems likely that native South American species could
252 also be cultured. A less satisfactory risk mitigation strategy would be to thoroughly screen
253 imported colonies for disease, to prevent the accidental introduction of non-native bee
254 pathogens. This would require international agreement as to which diseases are likely to be
255 present and how best to detect them, and also independent screening of bees to ensure that
256 health standards were being met. However, such a strategy could not remove risks of
257 competition with native pollinators, disruption of plant-pollinator mutualisms, or guard
258 against the spread of as yet unknown bee diseases.

259 The predictions of the model have bleak implications for the native South American
260 species *B. dahlbomii*, formerly a common species throughout much of Chile and south
261 western Argentina, and the only bumblebee species indigenous to this part of the world. *B.*
262 *dahlbomii* is arguably the largest bumblebee species in the world, and is certainly the most
263 southerly. It is a very long-tongued species upon which a range of deep-flowered Andean
264 plant species rely for pollination, and hence its loss would be a particular tragedy. It has

265 disappeared from perhaps 70% of its range (Arbetman et al. 2012) as *B. terrestris* invades
266 southwards, and it is now found only in Tierra del Fuego and a relatively small area of the
267 adjoining mainland. The model suggests that conditions are suitable for *B. terrestris* to
268 continue to spread southwards to the tip of South America, encompassing the entirety of the
269 range of *B. dahlbomii*. Given the current speed of spread of *B. terrestris*, the extinction of
270 *B. dahlbomii* is likely to occur within the next 2-3 years.

271

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275 European Pollinators, www.step-project.net).

276

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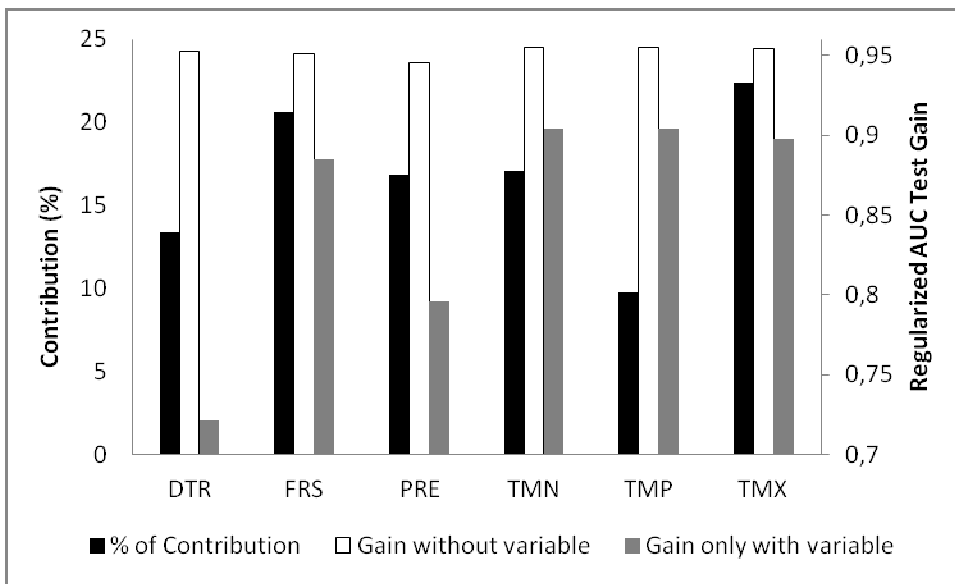
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375 **Figure 1.** AUC Jack-knife test gain, illustrating each variable's importance for Maxent.
376 The contribution of each variable to the model is represented by the black bars. The other
377 bars represent the jack-knife results for the model with only one variable (white) or with all
378 variables but the analysed one (grey). Values for the jack-knife results are represented on
379 the right axis. DTR = mean annual diurnal temperature range; FRS = frost days; PRE =
380 mean annual precipitation; TMN = mean annual minimum temperature TMP = mean
381 annual temperature; TMX = mean annual maximum temperature.

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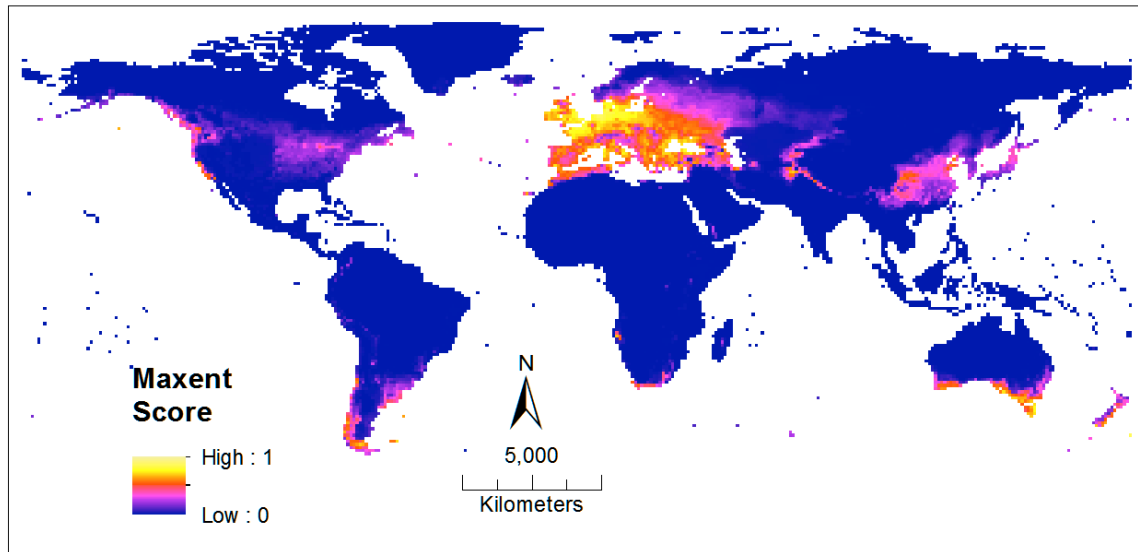


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385 Figure 2. Global climate suitability map for *B. terrestris* as calculated by MAXENT, based
386 on the native, western Palearctic distribution.

387

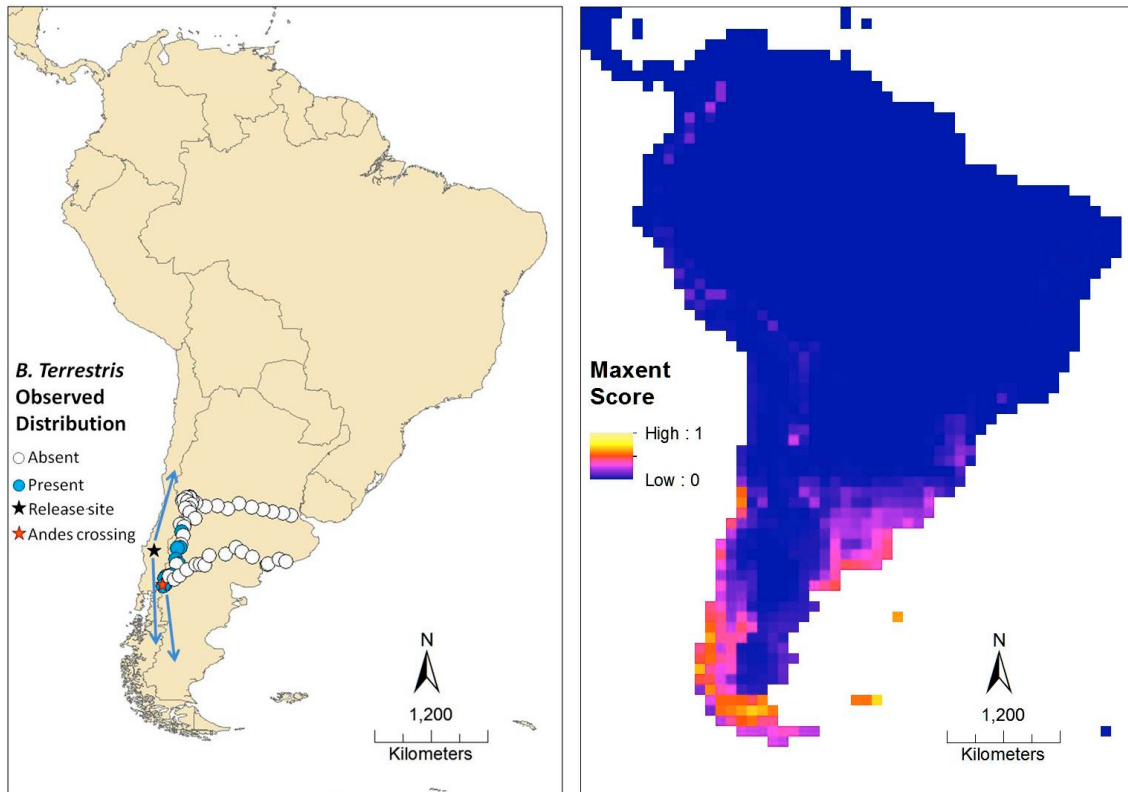


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389

390 Figure 3. Known distribution of *B. terrestris* in Chile and Argentina (left). Circles indicate
391 presence or absence in January 2012. Blue arrows indicate approximate spread according
392 to Abrahamovitch et al. (2001); Montalva et al. (2011); Arbetman et al. (2012). The
393 climatic suitability map for *B. terrestris* modeled with Maxent (right) predicts the likely
394 final extent of the invasion in South America. The known distribution of *B. dahlbomii*
395 approximates closely to the areas predicted to be suitable for *B. terrestris* in Chile and
396 western Argentina.

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