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Are range limits concordant with climatic niche requirements in alien plants: using leguminous invasive plants as case study, along latitudinal gradients, central Chile

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1 **Are range limits concordant with climatic niche requirements in alien**
2 **plants?: leguminous invasive plants as case study, along a latitudinal**
3 **gradient, central Chile.**

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12 **Abstract**

13 How do species reach the limits of their distribution and what prevents their
14 continued expansion beyond these ranges? Exotic plant species represent a natural
15 experiment to answer these questions. If climate is the limiting factor, then one would
16 expect a matching between the observed range limit for a species and the range
17 limit predicted by its climatic niche. If there is no matching, then other factors such
18 as dispersal limitation, competition or facilitation come into play. In this work we
19 compared the predicted and observed range limits for eight exotic legume species:
20 *Acacia dealbata*, *Acacia melanoxylon*, *Cytisus striatus*, *Teline monspessulana*, *Ulex*
21 *europaeus*, *Lotus corniculatus*, *Trifolium suffocatum* and *Vicia villosa*, in a latitudinal
22 gradient in Chile. For the estimation of the observed range limit (North and South),
23 absence/presence data were obtained from 30° to 43.1° south latitude. For the
24 estimation of the predicted range limits, GBIF presence data were used to construct
25 the global climatic niches, identifying suitable climatic zones (presences) and
26 unsuitable climatic zones (absences). With this information, presence probability

27 models were constructed with hierarchical Huisman-Olff-Fresh (HOF) regression,
28 from which the predicted range limits (North and South) were obtained. Our results
29 suggest that the species *Acacia dealbata* and *Cytisus striatus* have reached their
30 predicted edge at the northern and at the southern end of the gradient. The rest of
31 the species have not yet reached this limit across both geographic edges. At the
32 southern end of the gradient, most species have not reached the limit predicted by
33 the climatic niche; except for *Cytisus striatus* whose observed range limit is higher
34 than predicted. Factors other than climate, are discussed to explain the
35 discrepancies between observed and predicted range limits.

36

37 **Introduction**

38 Charles Darwin (1957) provided the first hypothesis to understand the factors that
39 set limits to species geographic distribution; he proposed that abiotic factors
40 (climate) are important at the abiotic stressful limits of distribution while species biotic
41 interactions become more important at the more benign extreme of the distribution.
42 Nowadays, this framework plays a central role in modern biogeography (Gaston
43 2003, Sexton et al. 2009) and is assumed a ubiquitous biogeographic pattern
44 (Louthan et al. 2015). New reformulations have proposed to understand range limits
45 of species (Ettinger and HilleRisLambers 2017, 2017, Sirén and Morelli 2020,
46 Paquette and Hargreaves 2021), however, they maintain the basic concepts
47 proposed by Darwin.

48 Hargreaves et al. (2014) proposed a hierarchical approach to understand range
49 limits using the climatic niche of species. This framework predicts the climatic niche

50 limits (CNL) i.e. the geographic limits predicted from climatic niche and compares it
51 with the range limit (RL), i.e. the observed limits in the extremes of distribution. If RL
52 $- CNL = 0$, populations located at the limit range, perfectly match between climatic
53 niche requirements and the extreme of distribution; 2) $RL - CNL < 0$; beyond RL
54 there are suitable habitats, but they cannot be colonized by species due to dispersal
55 limitation, introduction time or negative biotic interactions (competition, predation);
56 3) $RL - CNL > 0$, in RL populations are occupying unsuitable habitats, they are sink
57 populations which must be continuously subsidized by individuals from source
58 populations in order to persist; another explanation is that species establish positive
59 interactions with other species, allowing expansion following facilitating species
60 (Badano et al. 2007, Arredondo-Núñez et al. 2009). Biological invasions, provide
61 useful insights to learn about dynamics of species range limits (Sexton et al. 2009).
62 Given that invasive species, may have colonized habitats quite different to those
63 existing in their native ranges, we have a natural experiment to examine whether the
64 new range limits depart from expectations from climatic requirements (Keane and
65 Crawley 2002, Gaston 2003, Goncalves et al. 2022).

66 Climatic niche analysis has been prolifically used to understand the biogeography of
67 biological invasions (Peterson 2003, Thuiller et al. 2005, Broennimann et al. 2007,
68 Reed et al. 2008, Gallagher et al. 2010, Peña-Gómez et al. 2014, Cabra-Rivas et al.
69 2016). The global climatic niche enables to explore the climatic potentialities of
70 species using the totality of occurrences recorded for the species (Gallien et al. 2012,
71 Taucare-Ríos et al. 2016). In this study, we assessed if RL is within the variation of
72 CNL using global climatic niche. We applied this methodology to a set of eight exotic

73 leguminous plants species, invasive in Central Chile and in other regions of the world
74 (Quiroz et al. 2009). We also discussed its applicability to other biogeographic
75 situations and to what extent the hypothesis proposed by Hargreaves et al. (2014)
76 give us clues about the geographic dynamics of these eight species.

77 **Methods.**

78 *The setting*

79 Central Chile concentrates an interesting vascular flora; due to its high degree of
80 endemism and the intense deterioration of ecosystems, this region has been
81 considered a "hotspot" of biodiversity (Armesto et al. 1998, Myers et al. 2000). The
82 notable climatic gradient existing in Central Chile (decrease of temperatures and an
83 increase of precipitations (Di Castri and Hajek 1976, Di Castri 1991) constitutes an
84 ideal scenario to conduct a natural experiment to test biogeographic hypothesis. We
85 will use this climatic gradient to examine distribution responses of invasive species
86 belonging to the Family Leguminosae along Central Chile.

87 Chile has approximately 690 species of introduced plants (15% of the total flora,
88 Arroyo et al. 2000), being 70% of them of Eurasian origin (Matthei 1995). These
89 species are spreading into areas with native vegetation, thus affecting the
90 composition and structure of natural communities (Pauchard and Alaback 2004,
91 Bustamante and Simonetti 2005). Approx. 60% of human population is concentrated
92 in central Chile. There is an intensive land use, deforestation and habitat
93 fragmentation, all these factors regarded the drivers of biological invasions (Arroyo
94 et al. 2000). During the last years studies of plant invasion in Central Chile have

95 increased significantly (Arroyo et al. 2000, Sax 2002, Pauchard and Alaback 2004,
96 Bustamante and Simonetti 2005, Castro et al. 2005, Peña-Gómez and Bustamante
97 2012, Fuentes et al. 2014, Peña-Gómez et al. 2014, Montecino et al. 2016). Up to
98 date, we have a reasonable knowledge about the diversity of exotic species in Chile,
99 however, their biogeography is quite limited (Fuentes et al. 2013, but see Peña-
100 Gómez et al. 2014, Montecino et al. 2016). Data base about the presence of invasive
101 plants for Chile is limited and the estimation of range limits is only qualitative and at
102 a very coarse spatial scale. Fuentes et al. (2014) presented an update about the
103 magnitude of plant invasion in Chile. This information, concomitantly with a recent
104 book (Fuentes et al. 2014) was used to select the eight exotic species of this study
105 which are described ranging between 30° and 42° latitude.

106 Among the numerous exotic species recorded for Central Chile (Fuentes et al. 2014),
107 we decided to work with exotic trees, shrubs and herbs of the Family of Fabaceae
108 (Leguminosae). These species are regarded invasive in different parts of the world
109 (Ndlovu et al. 2013, Richardson et al. 2015) and most of them have produced
110 significant ecological impacts in Chile (García et al. 2014, 2015). Taxonomically,
111 these species are well known, its distribution has been documented for Central Chile
112 and are conspicuous component of anthropogenic landscapes. The species
113 selected for this study are *Acacia dealbata*, *Acacia melanoxylum*, *Cytisus estriatus*,
114 *Teline monpessulana*, *Ulex europaeus* and *Lotus corniculatus* as well as two
115 herbaceous species, *Trifolium soffocattum* and *Vicia villosa*

116

117

118 *Global climatic niche*

119 Global occurrences (presences) for the eight exotic species were obtained from
120 Global Biodiversity Information Facility (GBIF); the Atlas of Living Australia (ALA),
121 Biological Information Serving Our Nation (BISON), EcoEngine, Integrated Digitized
122 Biocollections (iDigBio) and iNaturalist" (iNat). Occurrence were selected if they had
123 an error less than 1 km. Local occurrences were recorded from 30° to 43° south
124 latitude (Figure 1), using two transects, one located along the coast and the other,
125 at the Central valley. We disposed plots (2 × 50 m), placed along the verge of
126 secondary or tertiary roads, with low management practices; roads are adequate
127 sampling sites as they are the most obvious corridors for the spread of invasive
128 species (Von der Lippe and Kowarik 2008, Barros and Pickering 2014, Van Der Ree
129 et al. 2015). Each plot was located each 10 km encompassing a total of 264 plots
130 (132 plots per transect). We collected plant samples for further identification in the
131 lab. From this information, we estimated the Observed northern and southern Range
132 Limits (NRL and SRL respectively), each properly georeferenced; they were
133 obtained empirically recording the last presence for each species at the extremes of
134 latitudinal gradient.

135 For the estimation of global climatic niche, we used the climatic grid procedure
136 (Broennimann et al. 2012). This method allows the visualization of the climatic niche
137 in a multidimensional space, obtained from Principal Component Analysis (PCA).
138 Specifically, we used this method as follows: (i) we generated 10.000 geo-referenced
139 random points to depict the global climatic environment; (ii) we also generated 5300
140 geo-referenced random points to depict the climatic environment in Chile; the

141 generation of random points was used through QGIS (versión 3.6.1); for climatic
142 characterization, from each of the random points, we extracted climatic variables
143 obtained from Worldclim 2.0, 1 km² resolution (Fick and Hijmans 2017); this data
144 base includes 19 climatic variables of precipitation and temperature, averaged from
145 1970 to 2000; finally, we correlated climatic data with random points through PCA,
146 thus generating the climatic grid (Broennimann et al. 2012). We identified four
147 regions in the climatic grid (multivariable climatic space): (i) global species
148 occurrences which represent global niche; (ii) the 10.000 random points, depicting
149 the global climatic environment; (iii) local species occurrence which represents local
150 niche in Chile; (iv) the 5300 random points depicting the climatic environments in
151 Chile (Figure 2). For the purposes of this study, we focused on regions (i) and (iv).
152 Using these two regions, we could define suitable and unsuitable climatic habitats in
153 Central Chile; suitable climatic habitats occur in the intersection between the global
154 climatic niche and the climatic environment in Chile while unsuitable climatic
155 habitats, occur into the climatic environment that is outside the global climatic niche
156 (for more details see Figure 2).

157 *HOF Curves*

158 For each zone (zone A and B), we collected randomly 25% of the total existing
159 points. Points selected from zona A were assigned 1 (suitable) while points selected
160 from zone B were assigned 0 (unsuitable). The sampling procedure was repeated
161 50 times, and for every sample of points (0 and 1) we constructed HOF curves
162 (Oksanen and Minchin 2002); basically, HOF curves are logistic regression models
163 which represent species responses along environmental gradients; Given a sample

164 of suitable (1) and unsuitable (0) points (Figure 2), the best model was selected using
165 likelihood ratio tests or Akaike criteria (Ihaka and Gentleman 1996). HOF curves
166 provide a set of parameters which describe different curve characteristic; one of
167 them, the Outer Border defined by the gradient value where the response curve
168 reaches $\exp(-2)$ relative to the highest estimated response value (Heegaard 2002),
169 this estimates was considered CNL predicted from global climatic niche. Using
170 QGIS we extracted for each point their corresponding latitude to depict the response
171 curve throughout the latitudinal gradient.

172 For each species, we constructed 50 HOF curves, thus estimating 50 values for the
173 Northern and 50 values for Southern CNL. To explore the variability of the estimates,
174 we used these values to obtain a bootstrap distribution for each range with 10.000
175 random resampling with replacement. If the RL falls within 95% confidence interval
176 of bootstrap distribution of northern or southern CNL, we accept the hypothesis that
177 $RL - NL = 0$; otherwise, we reject it.

178 **Results**

179 *Acacia* species (*A. dealbata* and *A. melanoxylon*) presents the broadest latitudinal
180 range in Chile (Table 1); *A. dealbata* was the species with a higher number of
181 presence records in the field (Table 1). On the other hand, *Trifolium suffocatum* was
182 the species with the lowest latitudinal range and one of the species with lowest
183 number of presence records in the field census in Chile (Table 1).

184

185

186 Table 1. Number of local presence/absence records per species and global
 187 presence records from GBIF (Global Biodiversity Information Facility).

| Species | Presence/absence points in Central Chile | | | | Latitudinal observed range (Decimal Degrees). In parenthesis: latitudinal range. | Global presence points |
|-------------------------|--|---------------|-----------------|----------------|--|------------------------|
| | Presence Coast | Absence coast | Presence valley | Absence valley | | |
| <i>A. dealbata</i> | 92 | 32 | 85 | 46 | (-32, -43.1) (11.1°) | 1141 |
| <i>A. melanoxilum</i> | 74 | 57 | 76 | 55 | (-32, -42.9) (10.9°) | 1313 |
| <i>C. striatus</i> | 31 | 100 | 27 | 104 | (-33.1, -41.4) (8.3°) | 740 |
| <i>T. monspessulana</i> | 51 | 80 | 38 | 93 | (-32.9, -41.1) (8.2°) | 318 |
| <i>U. europaeus</i> | 47 | 84 | 36 | 95 | (-35.6, -43.0) (7.4°) | 540 |
| <i>L. corniculatus</i> | 24 | 107 | 21 | 110 | (-33.4, -43.1) (9.7°) | 2105 |
| <i>T. soffocattum</i> | 0 | 131 | 2 | 129 | (-34.6, -35) (0.4°) | 682 |
| <i>V. villosa</i> | 1 | 130 | 3 | 128 | (-32.9, -36.9) (4.0°) | 1888 |

188

189 For the northern of distribution, we found that in only two species (*Acacia dealbata*
 190 and *Cytisus striatus*), we detected a matching between the observed and predicted
 191 north range limit (Table 2) while for the rest of species the observed north range limit
 192 was significantly lower than predicted (Table 2); for the southern distribution, we
 193 found matching between observations and predictions only for *Acacia dealbata* and
 194 *Cytisus striatus*; for *Acacia melanoxilum*, observed RL was lower than expected and
 195 for the rest of species the observed southern range limit was significantly higher than
 196 predictions (Table 2, Figures 3-4).

197 Table 2. Comparison between RL and CNL at the northern limit. CNL is represented
 198 by latitude values from 0.025 and 0.975 percentile (Q). For the northern limit the
 199 comparison has three possibilities: (i) RL = CNL, climate is enough to explain this
 200 limit; (ii) RL < CNL: competition and dispersal limitation explains this limit; (iii) RL >
 201 CNL: facilitation explains this limit.

| Specie | Q _{0.025} | Q _{0.975} | RL | RL - CNL | Hypothesis |
|-------------------------|--------------------|--------------------|--------|----------|----------------------------------|
| <i>A. dealbata</i> | -30.37 | -33.89 | -32.0 | RL = CNL | Climate |
| <i>A. melanoxilum</i> | -30.80 | -30.92 | - 32.0 | RL < CNL | Competition/dispersal Limitation |
| <i>C. striatus</i> | -32.18 | -34.62 | -33.1 | RL = CNL | Climate |
| <i>T. monspessulana</i> | -31.06 | -31.17 | -33.1 | RL < CNL | Competition/dispersal limitation |

| | | | | | |
|------------------------|--------|--------|-------|----------|----------------------------------|
| <i>U. europaeus</i> | -32.27 | -32.40 | -36.1 | RL < CNL | Competition/dispersal limitation |
| <i>L. corniculatus</i> | -18.96 | -19.21 | -38.7 | RL < CNL | Competition/dispersal limitation |
| <i>T. soffocattum</i> | -30.33 | -31.76 | -34.7 | RL < CNL | Competition/dispersal limitation |
| <i>V. villosa</i> | -21.61 | -25.60 | -32.9 | RL < CNL | Competition/dispersal limitation |

202

203 Table 3. Comparison between CNL and RL observed at the southern limit. CNL is
 204 represented by latitude values from 0.025 and 0.975 percentile (Q). For the southern
 205 limit, the comparison has three possibilities: (i) RL = CNL: climate is enough to
 206 explain this limit; (ii) RL < CNL: facilitation explains this limit; (iii) RL > CNL:
 207 competition and dispersal limitation explain the limit.

208

| Species | Q _{0.025} | Q _{0.975} | RL | RL - CNL | Hypothesis |
|-------------------------|--------------------|--------------------|-------|----------|----------------------------------|
| <i>A. dealbata</i> | -43.32 | -45.02 | -43.1 | RL = CNL | Climate |
| <i>A. melanoxilum</i> | -42.71 | -42.82 | -42.9 | RL < CNL | Facilitation |
| <i>C. striatus</i> | -40.72 | -42.29 | -41.4 | RL = CNL | Climate |
| <i>T. monspessulana</i> | -45.51 | -45.61 | -41.1 | RL > CNL | Competition/dispersal limitation |
| <i>U. europaeus</i> | -49.08 | -49.15 | -43.0 | RL > CNL | Competition/dispersal Limitation |
| <i>L. corniculatus</i> | -47.60 | -47.80 | -43.1 | RL > CNL | Competition/dispersal Limitation |
| <i>T. soffocattum</i> | -38.33 | -40.77 | -35.0 | RL > CNL | Competition/dispersal Limitation |
| <i>V. villosa</i> | -53.64 | -54.37 | -36.9 | RL > CNL | Competition/dispersal Limitation |

209

210 Discussion

211 The geographic position of RL was quite similar between Northern and Southern
 212 distribution; at the Northern range, in only two species (*Acacia dealbata* and *Cytisus*
 213 *striatus*), the RL was explained by climate; for the rest of species, the RL was
 214 explained by other factors such as dispersal limitation or negative biotic interactions.

215 At the Southern ranges, *Acacia dealbata* and *Cytisus striatus*, the RL matched with

216 climatic expectation as well; in one species (*Acacia melanoxylon*], RL was explained
217 by facilitation and for the rest of species, RL was explained by negative biotic
218 interactions and dispersal limitation.

219 For *A. dealbata* and *C. striatus*, climate explained RL either at the northern and at
220 the southern border. This matching may indeed be attributed to their high ornamental
221 value and widespread cultivation in parks, gardens and road borders, with strong
222 anthropogenic subsidies in terms of resources and conditions (Van Kleunen et al.
223 2018, Beaury et al. 2023). This increased human-mediated dispersal and cultivation
224 likely enhance their chances of expansion, allowing them to reach the maximum
225 extent of their distribution without dispersal limitation. *A. dealbata* is regarded one
226 of the most successful exotic trees in Central Chile with significant impacts on native
227 biodiversity (Fuentes-Ramírez et al. 2011). Our results give support to this invasive
228 success. Firstly, its niche requirements match with prevailing climatic conditions; (ii)
229 there is no dispersal limitation; (iii) it is a strong competitor over native plants due to
230 allelopathic effects on the germination and growth of seed and seedlings (Aguilera
231 et al. 2015) and a faster growth rate relative to native trees (Fuentes-Ramírez et al.
232 2011). However, there are some ecological constraints that can limit further
233 expansion because it has resulted the most attacked exotic plant by herbivorous
234 insects in invaded ranges (Rodríguez et al. 2009) which in turn can be used by
235 biological control in different parts of the world (Wilson et al. 2011, Wilgen et al.
236 2023).

237 At the southern extreme, *Cytisus striatus* also matched RL with climatic niche. This
238 result may be attributed to a low cold or freezing resistance of this species, as it has

239 been documented for this species in the northern hemisphere (Beans et al. 2012,
240 Thomas and Moloney 2013, Winde et al. 2020).

241 At the northern distribution, the abiotic environments are relatively hostile to plant
242 species. Under these conditions, plant-plant facilitation should be promoted,
243 according to theory (Bertness and Callaway 1994, Lortie and Callaway 2006);
244 however, we did not find evidence of such mechanism. We suggest that the
245 mismatch detected between observation and expectation for six species (Table 1)
246 can be attributed to dispersal limitations (low propagule pressure] due in part to a
247 relatively low human settlements (González and Rodríguez 2006). The southern end
248 of the climatic gradient in turn, hosts a high plant species diversity in Chile as well
249 as an increase of the forest biomass (Bannister et al. 2012). This increased diversity
250 may render these communities less invasible due to biotic resistance or competitive
251 mechanisms that limit the establishment of invasive species (Levine et al. 2004, Guo
252 et al. 2023). Our results are consistent with Callaway's hypothesis (Bertness and
253 Callaway 1994, Lortie and Callaway 2006), who suggests that less hostile
254 environments, such as the southern border, may induce higher competitive pressure
255 on exotic plants, thus resulting in constrained expansion of exotic plants further
256 south. In summary, we propose that dispersal limitation may play an influential role
257 at the northern border, while competition is more important at the southern border.
258 Further field experiments are needed to test these biogeographic hypotheses.

259 In the southern region, *Acacia melanoxylon*, exhibited its RL beyond predictions from
260 climatic niche. Mechanisms such as facilitation by human use, potential nurse
261 species interactions, or local adaptation and expansion of tolerance ranges may

262 explain these patterns. For example, a study by Turner et al. (2015) about invasive
263 thistle (*C. diffusa*) suggest that the physiological tolerances of *C. diffusa* may have
264 expanded in the invaded range. Invasive species tend to present adaptive plasticity
265 and niche expansion (Moran and Alexander 2014, Pack et al. 2022). These
266 hypotheses warrant further investigation through transplant experiments to elucidate
267 the underlying mechanisms driving these distribution patterns.

268

269 The study of the causal factors that explain RL along environmental gradients, has
270 proven to be a fruitful research program linking biogeography, ecology and evolution
271 (Holt and Keitt 2005, Sexton et al. 2009, Louthan et al. 2015). Most efforts have been
272 addressed to designing proper field experiments to discern among microevolutionary
273 and ecological factors responsible for such limits (Geber 2011, Hargreaves et al.
274 2014, Sexton and Dickman 2016); however less effort has been devoted to inferring
275 RL from climatic niche using statistical techniques. The method applied in this study,
276 proposes a methodology to infer statistically, the expected range limits based on
277 climatic niche requirements; this method establishes the geographic position species
278 range limits, then allowing us to dispose with precision where to put transplants
279 experiments to test biogeographic hypotheses proposed by Hargreaves et al.
280 (2014).

281

282 **Conclusion**

283 In conclusion, our study sheds light on the interplay between observed range limits
284 and the global climatic niche for leguminous invasive plants in central Chile. While
285 the climate-based limitation hypothesis is partially supported, with only two species

286 showing concordance between niche and distribution at the northern and southern
287 edge, our findings suggest that climatic conditions alone do not fully explain
288 distribution patterns. This discrepancy between niche and distribution is particularly
289 notable in areas with favorable climatic conditions, such as the southern extreme of
290 the climatic gradient. Moreover, the idiosyncratic responses of species at both ends
291 of the gradient highlight the importance of species-specific attributes and invasion
292 processes that may influence distribution patterns. The complex interplay between
293 climate, human activities, and ecological factors underscores the need for further
294 research, particularly experimental studies, to validate and elucidate the underlying
295 mechanisms shaping invasive plant distributions in mountainous regions like central
296 Chile. Understanding these mechanisms is crucial for effective management and
297 mitigation strategies aimed at controlling the spread and impact of invasive species
298 in these ecosystems.

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518 **Figures**

519 Figure 1. Graphic representation of the points sampled (red) to register the
520 presence/absence of the eight exotic species of this study across central Chile.

521 Figure 2. Graphic representation of the climatic grid and global climatic niche to
522 identify suitable and unsuitable hábitats. (A) PCA with global climatic niches,
523 intersected with the regional scale (study area in central Chile) climate niche. Pink
524 cells: global climatic niche; green line: local climatic conditions in Central Chile; red

525 line: global climatic conditions. (B) Identification of suitable (black points) and
526 unsuitable conditions (white points) for the species in the study area in Chile. Figure
527 obtained from Goncalves et al., 2022 with permission of the authors).

528 Figure 3. Bootstrap distribution of Northern and Southern CNL, obtained from global
529 niche models, for *Teline monspessulana*, *Cirsium striatus*, *Acacia melanoxylon* and
530 *Acacia dealbata*, Central Chile.

531 Figura 4. Bootstrap distribution of Northern and Southern CNL, obtained from global
532 niche models, for *Trifolium suffocatum*, *Vicia villosa*, *Ulex europaeus* and *Lotus*
533 *corniculatus*, Central Chile.