Predicting weed distribution at the regional scale in the native range: environmental determinants and biocontrol implications of *Phyla nodiflora* (Verbenaceae)

A J SOSA*† (iD), M V CARDO†‡ & M H JULIEN§

*Fundación para el Estudio de Especies Invasivas (FuEDEI), Hurlingham, Provincia de Buenos Aires, Argentina, †Consejo Nacional de Investigaciones Científicas y Técnicas, Ciudad Autónoma de Buenos Aires, Argentina, ‡Ecología de Enfermedades Transmitidas por Vectores, Instituto de Investigaciones e Ingeniería Ambiental (3iA), Universidad Nacional de General San Martín, San Martín, Provincia de Buenos Aires, Argentina, and §CSIRO Ecosystem Science & Biosecurity Flagship, Brisbane, QLD, Australia

Summary

Alien plants produce severe environmental and economic losses in the territories they invade. Modelling the spatial distribution of alien species as a function of the environment in the native range has therefore become an essential first step in the struggle against invasions. *Phyla nodiflora* var. *minor* is a fast-growing perennial herb native to South America that has spread through three continents, where it poses a major threat to biodiversity and significantly impacts on conservation and grazing systems, mainly in riparian areas. To assess the distribution of native Argentine populations of *P. nodiflora* as a function of the environment, we conducted long-term roadside surveys and associated the occurrence of the plant with climatic, geographical, demographical and vegetation cover variables in a generalised linear mixed model. The plant was recorded in 230 of 431 sites, mostly east of 66°W and north of 39°S. According to the best model, which predicted the data 58% better than random assignment, its occurrence was associated with temperature variables (mean annual values and daytime range) and relative humidity. Based on these associations, we generated a presence probability map for the occurrence of *P. nodiflora* in southern South America. Understanding the environmental determinants of the distribution of weeds in their native range provides valuable baseline data to further manage the spread of alien species.

Keywords: biological control, modelling, invasive species, spatial dynamics, distribution.

Introduction

Plant invasions are a serious threat to natural and managed ecosystems worldwide (Manchester & Bullock, 2000). Invading species degrade human health and wealth, alter the structure and functioning of undisturbed ecosystems and threaten native biological diversity (Vitousek *et al.*, 1997). In this context, the increasing need to understand and manage plant invasions has generated interest in predicting the

Correspondence: A J Sosa, Fundación para el Estudio de Especies Invasivas, Simón Bolivar 1559 (B1686EFA), Hurlingham, Provincia de Buenos Aires, Argentina. Tel: (+54) 1146620999 ext. 119; Fax: (+54) 1146620999 ext. 104; E-mail: alejsosa@fuedei.org

distribution of weeds in both anthropogenic and natural systems (Peltzer *et al.*, 2007). Spatial modelling of species distributions has therefore become a central tool in the study of biological invasions, placing predictive modelling of species occurrence as a function of the environment at the forefront of invasion research (Steiner *et al.*, 2008).

The problem of invasive alien plants that are likely to have an adverse environmental or economic effect on their invaded ranges is frequently addressed by different weed management strategies, biological control among them. This consists in the deliberate introduction of host-specific insects or pathogens that reduce the plant's ability to invade. Potential biocontrol candidates are subjected to rigorous specificity tests to minimise the risks of direct or indirect non-target effects. Under these conditions, the method is considered safe, environmentally sound and cost-effective (Cruttwell McFadyen, 1998). The first step of any weed control programme therefore involves native-range surveying, that is searching for the weed and its naturally co-occurring enemies in the region of origin. Consequently, the identification and characterisation of the native range and the centre of origin of a weed are crucial in all biological control programmes (McClay *et al.*, 2004).

Phyla nodiflora var. *minor* (Hook.) O'Leary & Múlgura (ex. *P. canescens* (Kunth) Greene) is a fast-growing member of the Verbenaceae, a mat-forming perennial herb that develops on floodplains and in pastures, mainly in heavy clay soils, but also in lighter and sandier soils. It reproduces sexually and vegetatively, both in association with water; the seeds require inundation to be released from dormancy, whereas clonal plant fragments are dispersed by water courses. It can also tolerate long periods of inundation and drought or frost conditions (Macdonald *et al.*, 2012). Such adaptability has been taken into consideration when modelling its potential distribution in Australia under different climate change scenarios (Murray *et al.*, 2012).

The weed is native to South America, distributed from southern Ecuador, throughout Peru, Paraguay, Bolivia and Brazil, to Chile, Argentina and Uruguay (O'Leary & Múlgura, 2011). It has also been recorded from fossil pollen in Argentina (Stutz *et al.*, 2014), reinforcing this area as the centre of origin. Commonly referred to as Lippia, the species is found worldwide in tropical to temperate regions (O'Leary & Múlgura, 2011). In Australia, it poses a major threat to biodiversity and riparian areas and has a significant impact on conservation and grazing systems, due to its increasing density and distribution (Julien *et al.*, 2004). The greatest impact occurs in the Murray Darling Basin, costing $38 million per year to the grazing industry and producing an estimated annual loss of environmental services of $1.8 billion (Earl, 2003). There, biological control has been proposed as part of its management, particularly in reserve areas, woodlands, forests and along stream banks.

The quantification of the species–environment relationship through models may be regarded as hypotheses as to how environmental factors control the distribution of species (Guisan & Zimmermann, 2000). In this study, we assessed the distribution of native populations of *P. nodiflora* in Argentina as a function of the environment. To do so, we developed an approach combining field surveys, geographic information systems (GIS) and generalised linear mixed models (GLMM) to generate a spatial model for the distribution of plant populations in southern South America. The main objectives were to identify the environmental variables that affect the distribution of *P. nodiflora* in its native range and to obtain a presence probability map. Such a map can contribute to select areas where one should search for potential biological control agents in the native range. Finally, we aimed to discuss aspects hampering the search for such biological control agents for *P. nodiflora* and their potential applications to the introduced range, within an integrated weed management programme.

Materials and methods

Study area

Continental Argentina extends from 21°46′S to 55°03′S and 53°38′W to 73°34′W, with a surface of 2 791 810 km^2 distributed in 23 provinces and the Federal District (Fig. 1). The country encompasses several climatic regions from subtropical in the north to cold temperate in the south. Autochthonous vegetation is highly variable throughout the territory, which leads to the definition of 11 phytogeographical regions (Cabrera, 1976). The population is approximately 40 million people with >60% concentrated in three provinces, namely Buenos Aires, Córdoba and Santa Fé (INDEC, 2010).

Phyla nodiflora has been recorded throughout Argentina, in 17 provinces. The weed *P. nodiflora* var. *minor*, originally known as *P. canescens*, was recently included as a variety of *P. nodiflora*, along with other two varieties (*P. nodiflora* var. *nodiflora* and *P. nodiflora* var. *reptans*) and possible intermediate forms (O'Leary & Múlgura, 2011). In its exotic range in Australia, the plant is sometimes confused with *P. nodiflora* var. *nodiflora* (Xu *et al.*, 2015). For further analyses in this work, all varieties were pooled and hereafter referred to as *P. nodiflora* following O'Leary and Múlgura (2011).
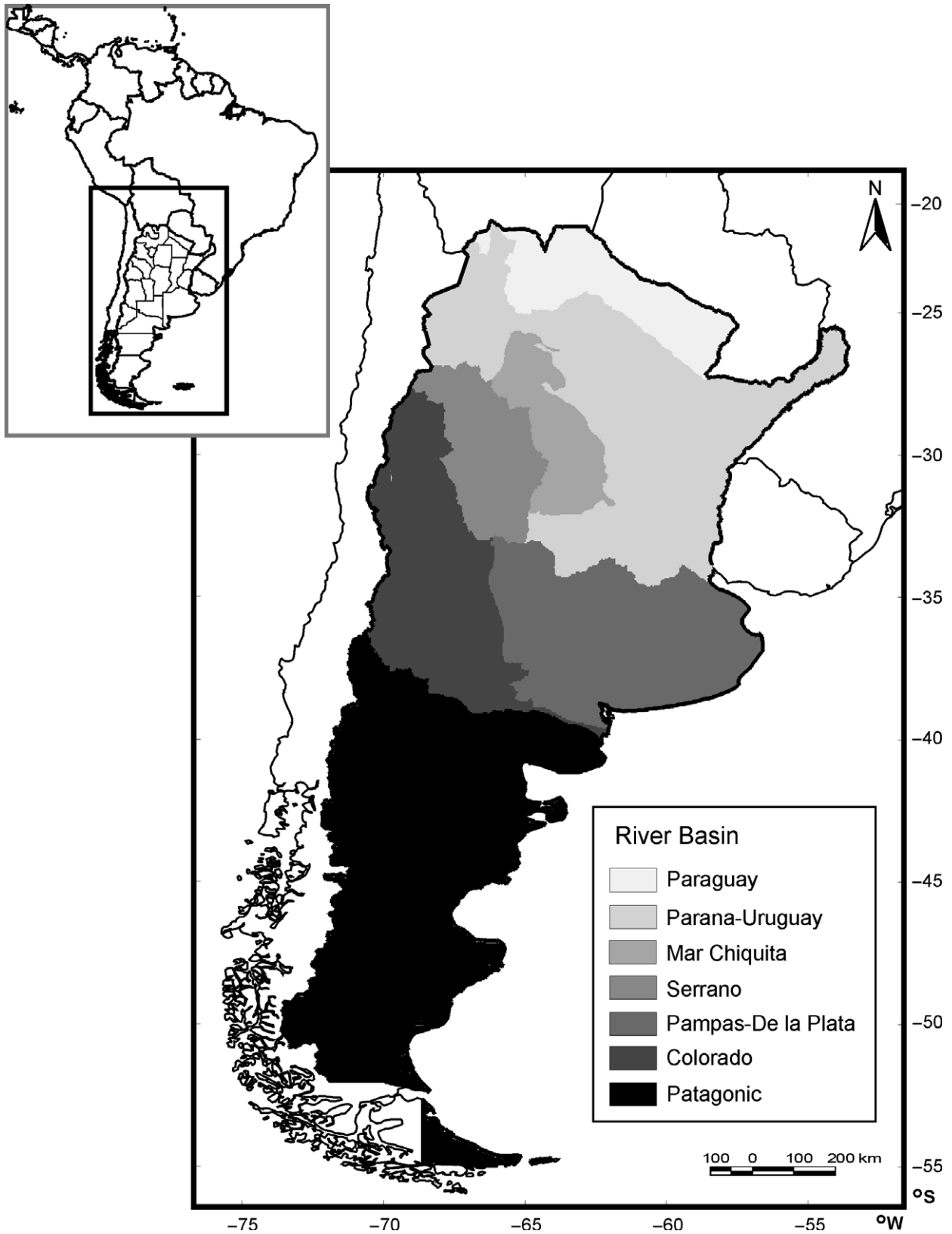
Fig. 1 Main river basins considered for the modelling of *Phyla nodiflora* within its native range in Argentina.

Field surveys

In Argentina, roadside surveys were conducted from 41°S northwards from December 2004 to January 2011. As the plant is small and prostrate and often grows in the understory, it is difficult to see from a moving vehicle. Therefore, stopping inspection sites were assigned according to the following criteria: the first stopping site was randomly selected within the first 50 km away from Buenos Aires along main routes and subsequent inspections were systematically placed every 50, 100 and 180 km, giving a total of 431 visited sites. Additionally, in December 2007, a survey was conducted in Chile along a North–South transect from Copiapó (27°22′S, 70°20′W) to Valdivia (39°49′S, 73°17′W). There, sampling was conducted in locations with previous herbarium records, about every 50 km along the transect and in river beds, where the habitat is suitable for plant growth. In all cases, each stopping site was thoroughly scanned for the occurrence of the weed in a fixed area of approximately 100 m along the road × 3 m wide. If present, taller herbaceous plants were set aside to search beneath them, near the ground. Plant specimens from all locations were collected and dried for further identification.

Geographical database

Data on the occurrence of *P. nodiflora* were georeferenced in a GIS. Although the search criterion was to stop at 50 km in each survey, several surveys were conducted each year, and the main routes inspected were repeated in some surveys performed in different years. Therefore, when pooling all surveys, some sampling pairs were closer than 50 km to each other. Given the fact that local absences near positive records may be due to stochastic factors or unmeasured microenvironmental features, to evaluate a potential spatial autocorrelation a semivariogram of the data set was performed (Creesie, 1993). The range was approximately 40 km, therefore negative points within a 40 km radius of a positive point were excluded from further analyses. This led to the exclusion of 115 negative points; in the resulting subset of 316 sampling sites, *P. nodiflora* was present in 219 sites and absent in 97.

Distribution model

We used GLMM to analyse the relationship between the distribution of *P. nodiflora* and the environment. The model was fitted using a maximum likelihood method, assuming a binomial distribution of errors and applying the logistic function as a link between the response variable and the linear predictor (McCullagh & Nelder, 1989).

Presence/absence of *P. nodiflora* per sampling site (*ca.* 300 m^2) was the response variable, whereas explanatory variables were selected based on previous information on the ecology and environmental requirements of the plant (Gross *et al.*, 2010; Xu *et al.*, 2010a). Thematic layers of each explanatory variable considered (see Table 1) were built in grid format covering the study area and its surroundings. Some variables (climatic features, percent vegetation cover and elevation above sea level) were directly available in grid format of dissimilar spatial resolution, ranging from 0.5 × 0.5 to 18.5 × 18.5 km (Table 1). Distance to permanent rivers and to any kind of river or water body were calculated from vector-based digital maps. Finally, demographic variables were available as points and interpolated using the inverse weighted distance method. The values of all environmental variables at each sampling site were obtained with the GIS to run the model.

Initially, the Wilcoxon 2-sample test was used to compare the values of each explanatory variable between sites grouped according to presence or absence of *P. nodiflora*. All continuous variables were then centred and squared and preliminary univariate GLM were run for each variable, either categorical or continuous and, in the latter case, for the sum of the variable and its square to account for any potential quadratic relationships (Table 1). Subsequently, a manual upward stepwise multiple regression procedure was performed. Term additions were evaluated by Akaike's Information Criterion (AIC) and the model that yielded the lowest AIC was selected from all possible models (Zuur *et al.*, 2009). Two-way interactions were evaluated in each step of the procedure. To deal with collinearity between explanatory variables, the variance inflation factors (VIFs) were calculated, and a combination of explanatory variables was considered valid if all VIF values were ≤5 (Zuur *et al.*, 2009). Once the most complete set of significant explanatory variables were selected, and to account for the dependence of *P. nodiflora* upon water courses for reproduction and dispersal, the river basin of each presence/absence register was entered as a random factor. In the final model, the presence of flowers and the sampling year were included as factors to control for differential effects of plant detection due to blossom or a particular trend in time, whereas latitude and longitude were also tested to discard any remnant spatial gradient not absorbed by the explanatory variables.

The presence probability distribution map was built by applying the final GLMM formula pixel to pixel in the GIS. Because of the deliberate 40 km exclusion

Table 1 Univariate statistics of the explanatory variables used to model distribution of *Phyla nodiflora* in Argentina. The Wilcoxon 2-sample test (Wilcoxon *P*) was used to compare the variables between sites grouped according to presence (PP) or absence (PA) of *P. nodiflora* generalized linear models parameter (B) and standard error (SE) are given for each univariate fit (*t*-test B/SE and 1 degree of freedom [df]) for continuous variables; chi-square test on the deviance and 1 df for the urban/rural factor. For continuous variables, best fit between linear (x) or quadratic relations ($x + x^2$) is reported. AIC of the null model is 391.7

Variable	Description	Units	Cell side (km)†	Data source	Wilcoxon P	PP median (min-max)	PA median (min-max)	B ± SE	AIC
Altitude	Elevation above sea level	m	1	1	**	203.5 (−33 to 2991)	96 (−37 to 2987)	0.00035 ± 0.00016*	385.9
Trees	Percentage of surface with tree cover	%	0.5	2	n.s.	10 (0 to 78)	9 (0 to 71)	n.s.	393.5
Herbs	Percentage of surface with herb cover	%	0.5	2	n.s.	85 (22 to 100)	83 (14 to 100)	n.s.	391.8
Bare soil	Percentage of surface with bare soil cover	%	0.5	2	n.s.	0 (0 to 54)	0 (0 to 86)	−0.033 ± 0.013**	386.4
Temperature	Mean annual temperature	°C	18.5	3	***	19.8 (10.3 to 23.5)	17.7 (5.7 to 22.4)	0.14 ± 0.04***	381.1
Amplitude	Mean annual daytime temperature range	°C	18.5	3	**	12.9 (9.8 to 16.3)	12.2 (10.6 to 16.1)	0.189 ± 0.095*	389.7
Precipitation	Mean annual cumulative precipitation	cm	18.5	3	**	67.5 (14.9 to 151.6)	79.5 (11.7.9 to 149.3)	***·‡	378.0
Humidity	Mean annual relative humidity	%	18.5	3	*	71.5 (53.9 to 79.8)	73.5 (46.8 to 79.9)	***·‡	366.8
Wind speed	Mean annual wind speed	m/s	18.5	3	***	2.7 (1.7 to 5.0)	3.0 (1.8 to 5.5)	***·‡	375.5
Frost	Annual frost days frequency	days	18.5	3	n.s.	15.7 (0.1 to 143.0)	22.3 (0.1 to 172.0)	−0.010 ± 0.004*	388.1
Wet days	Number of annual rainy days	days	18.5	3	*	83.6 (39.9 to 104.4)	85.5 (33.6 to 116.4)	***	369.0
River distance	Distance to the nearest river	km	12.6	4	n.s.	4.8 (0.3 to 170.7)	4.4 (0.2 to 140.1)	n.s.	392.9
Water distance	Distance to the nearest water body or course (excluding the sea)	km	12.6	4	**	3.0 (0.0 to 60.0)	2.0 (0.1 to 60.5)	*·‡	389.0
Population	Population counts in 2010	People	4.6	5	n.s.	147 (1 to 91554)	139 (0 to 3065)	n.s.	388.6
Rural/Urban	Factor specifying rural or urban areas§		0.9	5	n.s.			n.s.	393.7

n.s., not significant.

Data sources: (1) United States Geological Survey (2005) Center for Earth Resources Observation and Science (EROS). Shuttle Radar Topography Mission, Digital Terrain Elevation Data; (2) Hansen M, Defries R, Townshend JR, *et al.* (2003) 500 m MODIS vegetation continuous fields. The Global Land Cover Facility, College Park, Maryland; (3) NNDC Climate Data Online. http://www.nesdis.noaa.gov; (4) Subsecretaría de Recursos Hídricos (2002) Atlas digital de los recursos hídricos superficiales de la República Argentina. Subsecretaría de Recursos Hídricos, Presidencia de la Nación, Buenos Aires, Argentina; (5) Instituto Nacional de Estadísticas y Censos (2010) Censo Nacional de Población, Hogares y Viviendas 2010. http://www.censo2010.in dec.gov.ar/.

***Significant at *P* < 0.001; ** *P* < 0.01; * *P* < 0.05.

†Square cells.

‡Best fit is the sum of the variable and its square. In this case, no parameter estimators are provided and significance is the result of the ANOVA test comparing each model with the null model.

§The established national criterion defines as rural any area in which population is dispersed, or grouped in a locality of ≤2000 inhabitants. On the contrary, any area in which >2000 inhabitants live together is considered urban.

criterion, all points were forced to be either positive or negative within 40 km, therefore cell size of the output map could be no smaller than 40 km. The resulting map was smoothed with a 10 km moving window to improve the graphic quality of the final product. The software R version 3.2.3 (R Development Core Team, 2015) and Arcview GIS 3.2 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) were used for modelling and mapping, respectively.

Model validation

To evaluate the classification effectiveness of the selected model, the Cohen's Kappa coefficient (*K*) was calculated. This index assesses improvement of classification of the model over chance and overcomes the problem of unequal number of presences and absences (Fielding & Bell, 1997). The quality of the model was classified following the Landis and Koch (1977) ranges of agreement: poor $K < 0$; slight $0 \leq K \leq 0.2$; fair $0.2 < K \leq 0.4$; moderate $0.4 < K \leq 0.6$; substantial $0.6 < K \leq 0.8$; and almost perfect $0.8 < K \leq 1$. Given that the predicted values of the binomial model are a probability between 0 and 1, *K* was calculated for each 0.01 cut-off point between the whole range of possible values (0–1) and the point that provided the best value of *K* was reported as the optimal.

Finally, as an external validation data set, the presence probability according to the model for 64 *P. nodiflora* herbarium records from the Instituto de Botánica Darwinion (San Isidro, Buenos Aires, Argentina; ISSN 2250-6365) was calculated. Such records were registered from 1900 to 1970's, and included points throughout the South American native range of the plant, in Argentina, Chile and Uruguay.

Results

Phyla nodiflora was widely distributed across the landscape, in 56.6% (230/431) of the sampled sites. Its occurrence was registered mostly east of 66°W and north of 39°S, from sea level to 2100 m. Univariate comparison of sites with and without *P. nodiflora* showed significant differences for several of the environmental variables considered, with the remarkable exception of vegetation cover variables (Table 1). The univariate GLMs were fairly consistent with these results.

The best model described the distribution of the plant as a function of relative humidity and two temperature variables – annual mean and amplitude (Table 2). Flower and year factors were not significant suggesting that the results were not influenced by the sampling design. Latitude and longitude, along with their interaction, were also not significant. Optimal

Table 2 Generalised linear mixed model for the occurrence of *Phyla nodiflora* in Argentina. Parameters for each variable are given, along with their corresponding standard error (SE) and degrees of freedom (df). *Z* value = Parameter/SE. Quadratic terms are indicated with a superscript (^{2}) next to each variable. The river basin (seven groups) is included as a random factor. AIC of the final model is 300.6

| Variable	Parameter	SE	df	*Z* value
Intercept	1.529	0.549	1	2.784**
Humidity	−0.010	0.057	1	−0.177
Humidity^2	−0.018	0.005	1	−3.501***
Temperature	0.304	0.086	1	3.520***
Amplitude	0.481	0.221	1	2.171*
Amplitude^2	0.284	0.104	1	2.725**

***Significant at $P < 0.001$; **$P < 0.01$; *$P < 0.05$.

cut-off point was estimated at 0.55; this means that in any given site or pixel in the map in which the probability of occurrence is ≥0.55, *P. nodiflora* is predicted to occur. In contrast, plant presence is unlikely in any site/pixel with a value <0.55. *K* value was 0.58, classifying the predictive accuracy of the model as moderate.

Phyla nodiflora presence probability was higher in areas of intermediate relative humidity and high mean annual temperature, but with a relative minimum in zones with intermediate temperature amplitude (around 12°C, Fig. 2). The river basin (seven groups, Fig. 1) was a significant random factor. The presence probability of *P. nodiflora* was higher than for an 'average' basin (i.e. no correction of the linear predictor by random effects) in four basins (Pampas de la Plata, Patagonic, Paraguay and Mar Chiquita), whereas the opposite occurred for the other three (Paraná-Uruguay, Serrano and Colorado). For example, according to the model, *P. nodiflora* was predicted to occur in areas with a mean annual temperature of ~14.5°C to warmer areas in the average basin; however, it should be found in colder areas (~10°C) in Pampas de la Plata basin, but only from 20°C in Paraná-Uruguay basin (Fig. 2C).

In Argentina, the map of potential distribution shows a high occurrence probability along the north and centre of the country (Fig. 3), which falls towards the west all along the country and in a circumscribed zone in the north-east. The distribution gap around 31–32°S should be regarded with care, as there are few sampling sites within it. The map shows another zone of high probability of presence in the southern end of the country.

To generate a distribution probability map for the rest of southern South America (Chile, Uruguay and south of Bolivia and Paraguay), the model was extrapolated considering an average basin. With this approach, most records (64%, 7/11) from the survey in Chile which had not been utilised to build the model,
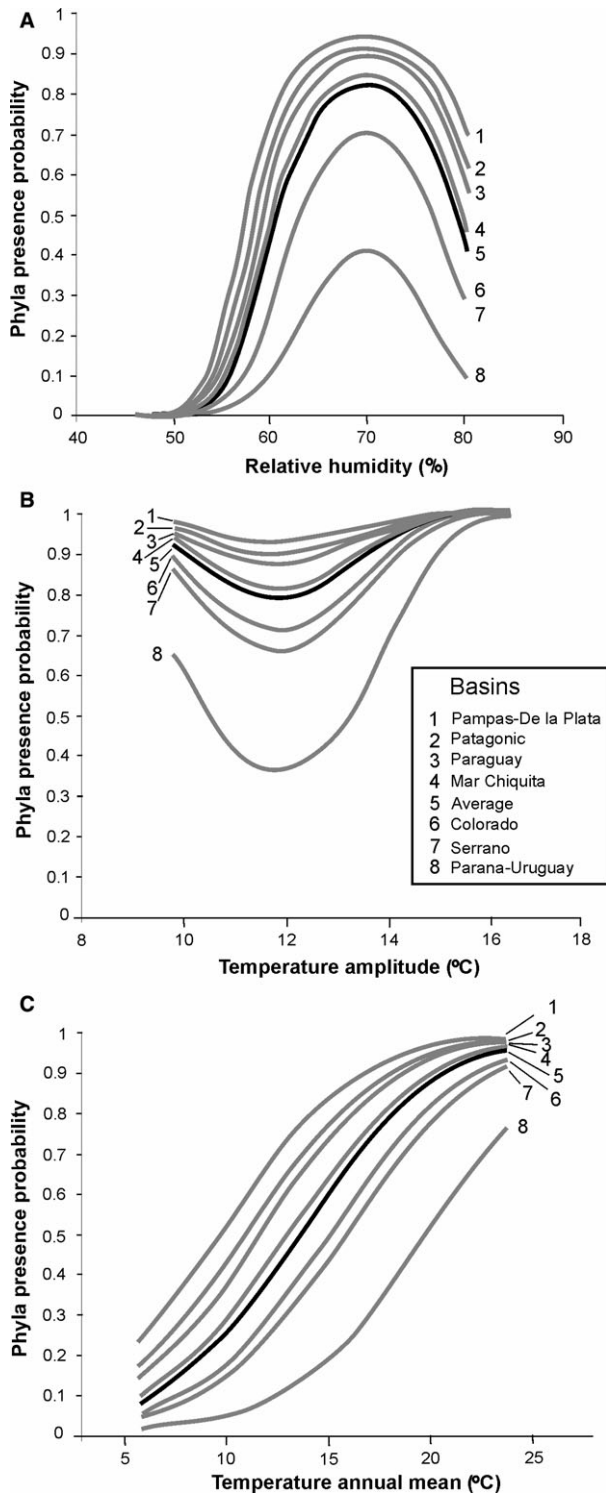
Fig. 2 Probability of presence of *Phyla nodiflora* as a function of varying values of each environmental variable included in the final generalised linear mixed model (A- relative humidity; B-mean temperature; C-temperature amplitude) at mean values of the other explanatory variables, for an 'average' basin (*i.e.* no random effect) and for each of the seven basins included as random factors.

were correctly classified (Fig. 3). In Chile, plants were associated with water courses in dry areas such as the Atacama Desert. South of the desert region, plants

were found along railway lines, roadsides, footpaths and in lawns. The samples were identified as either *P. nodiflora* var. *minor* or *P. nodiflora* var. *nodiflora*. They differed from Argentine populations in leaf toughness and colour and shape of the inflorescence (Sosa AJ & Julien M, unpubl. obs.).

Regarding the external validation data set, the percentage of correctly classified herbarium records was 51% (33/64), from which 27/55 were located within the range of the model data (Argentina) and 6/9 were located in neighbouring countries (Chile and Uruguay) (Fig. 3).

Discussion

Plant invasions are a leading cause of biodiversity loss for native communities, representing a significant threat to ecosystem function and economic sustainability (Cipriotti *et al.*, 2010). In this context, understanding the environmental determinants of the distribution of weeds in their native range is essential for proper management and control in introduced areas. This is hindered by the fact that acquisition of native range data is typically slow and expensive and the researcher may face different sorts of difficulties, such as time and budget constraints (Trethowan *et al.*, 2011). Data collected from diverse sources are also subjected to a variety of biases, depending on both the purpose and methodology of the register. Therefore, the exhaustive native range survey presented herein is valuable, due to its extent both in space and time, the record of absence points in addition to occurrence and the uniformity in data gathering.

The spatial distribution of weeds and its environmental associations can be analysed with GLMM, a statistical approach which has been reported to reach better models compared with other multivariate techniques, such as Canonical Correspondence Analysis (Guisan & Theurillat, 2000). The results presented herein show that the distribution of *P. nodiflora* can be modelled as a function of environmental variables to obtain a regional presence probability map. Given that the variables used are easily available, this kind of approach might also be extended to other regions and validated with external data sets in order to check for model accuracy. A word of caution is that the models predict the realised niche, rather than the fundamental niche of the plant, which depends on biological interactions in addition to environmental determinants (Trethowan *et al.*, 2011). Therefore, the same exact model need not apply for areas in which the weed was introduced. Care must be taken when exploring the potential for the spread of species in invasive regions; apart from being released from their natural enemies,
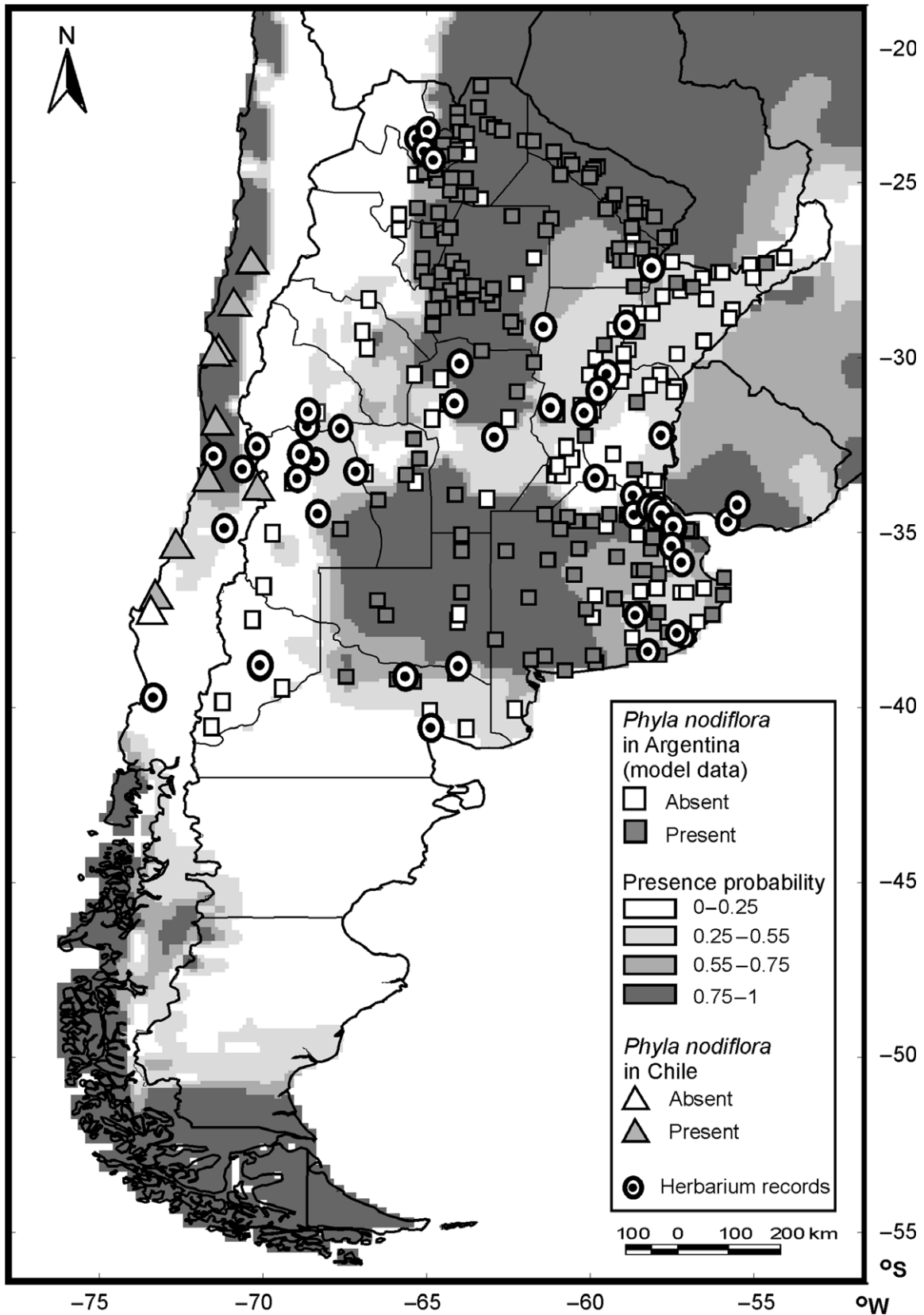
Fig. 3 Presence probability map of the distribution of *Phyla nodiflora* in southern South America, shown in a grey scale. Presence is predicted in areas with probability values higher than 0.55. Sites used for model development are indicated by squares and records in Chile are indicated by triangles (filled for presence and empty for absence of *P. nodiflora*). Validation sites (herbarium records) are plotted as circles.

weeds may not be at equilibrium with the climate and their niches may expand further (Beaumont *et al.*, 2009). Ideally, when modelling the potential distribution of invading species, data from both the native and introduced ranges should be used to account for both the niche evolved in the area of origin and the potential niche shifts associated with cross-continental transfer into abiotically and biotically different environments (Dullinger *et al.*, 2009).

Insight on the native range of an invasive species, including its geographical extension, could help to understand its invasiveness and enhance alternative management strategies, including biological control. For species in the family Cactaceae, Novoa *et al.* (2016) found that the native range size, particularly of the genus *Opuntia*, was correlated with both invasiveness and impact. They considered that invasive species that can establish and spread under a variety of conditions (and therefore become widespread in their native range) are able to successfully establish and become invasive when introduced to new regions. The native range of *P. nodiflora* is in South America (O'Leary & Múlgura, 2011), and genetic evidence suggests that this plant may be restricted to central and northern Argentina and similar latitudes in coastal Chile (Xu *et al.*, 2010b). Therefore, this is probably the centre of origin of this target weed, actually worldwide distributed, and where potential biological control candidates should be looked for.

However, it is difficult to define plant species limits and to properly identify a specimen of *Phyla* found in nature. In northern Argentina, *P. nodiflora* var. *minor* occurs along with *P. nodiflora* var. *nodiflora* and *P. nodiflora* var.*reptans* and probably some unknown hybrid combinations. Preliminary studies have shown that insects and pathogens seem to 'recognise' *Phyla* specimens from different localities as different plants, expressed as a differential feeding preference and larval performance (Sosa *et al.*, unpubl. obs.), but further studies are necessary to elucidate such patterns. Similar patterns have been recorded in other systems, such as the weevil *Stenopelmus rufinasus* that utilised only closely related *Azolla* species. While the plant taxonomy was only confirmed by molecular studies (Madeira *et al.*, 2016), these authors considered the weevil 'an excellent taxonomist'. On the other hand, populations of insect species that are widely separated in the native range should be evaluated as potential biocontrol agents with care, as they could belong to cryptic species (Paterson *et al.*, 2016). These considerations can dramatically affect the success of biological control programmes, for better or for worse.

For the prioritisation of biocontrol agents, frequency and host plant use of candidates should be studied. To anticipate and prevent potential non-target effects, host specificity, plant damage and geographical extensions in the plant native range should be considered, particularly for weeds composed by a complex of related species (Moffat *et al.*, 2013). In the case of *P. nodiflora*, we still cannot affirm that specimens from different localities in Argentina represent species or varieties (Xu *et al.*, 2015), or if such natural enemy–host plant associations respond to other mechanisms, such as local adaptation (Kawecki & Ebert, 2004). Genetic analyses, based on specific plant chemicals, isozymes and DNA, are currently being used as part of biocontrol programmes. These analyses sought to identify and characterise different strains of a given weed, to facilitate the collection of agents from the same strain and place of origin as the target weed (Cruttwell McFadyen, 1998). The taxonomical situation of *Phyla* as a genus is still unresolved due to inconsistencies in morphology (O'Leary & Múlgura, 2011) and genetics (Xu *et al.*, 2015). Any potential biocontrol candidate, particularly for management in Australia, undoubtedly needs to be tested against the Australian native populations of *P. nodiflora*.

Conclusions

Within its native range, the spatial distribution of *P. nodiflora* can be modelled as a function of the environment, notably with temperature and relative humidity. Expressed in a distribution map, these associations have two important applications in the struggle against weed invasion. They aid in the selection of areas within the native range in which to search for potential biological control agents and they may also help understand the potential spread of the weed in their invaded range. Natural enemies that could be utilised as biological control agents of *P. nodiflora* need to be sought in different areas of the native range. Such potential candidates need to be studied under different environmental scenarios and considering new genetic insights in plant taxonomy to get a better match between native and exotic ranges, to predict impact and to attain successful management.

Acknowledgements

References

Beaumont LJ, Gallagher RV, Thuiller W, Downey P, Leishman MR & Hughes L (2009) Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Diversity and Distributions* **15**, 409–420.

Cabrera AL (1976) *Regiones Fitogeográficas Argentinas*. Acme, Buenos Aires, Argentina.

Cipriotti PA, Rauber RB, Collantes MB, Braun K & Escartín C (2010) *Hieracium pilosella* invasion in the Tierra del Fuego steppe, Southern Patagonia. *Biological Invasions* **12**, 2523–2535.

Creesie NAC (1993) *Statistics for Spatial Data*. Wiley, New York, USA.

Cruttwell McFadyen RE (1998) Biological control of weeds. *Annual Review of Entomology* **43**, 369–393.

Dullinger S, Kleinbauer I, Peterseil J, Smolik M & Essl F (2009) Niche based distribution modelling of an invasive alien plant: effects of population status, propagule pressure and invasion history. *Biological Invasions* **11**, 2401–2414.

Earl J (2003) *The Distribution and Impact of Lippia (Phyla canescens) in the Murray Darling System*. Final Report to the Lippia Working Group. Agricultural Information & Monitoring Service, ABN: 73 918 506 894, Guyra, NSW, Australia.

Fielding AH & Bell JF (1997) A review of the methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**, 38–49.

Gross CL, Gorrell L, Macdonald MJ & Fatemi M (2010) Honeybees facilitate the invasion of Phyla canescens (Verbenaceae) in Australia – no bees, no seed!. *Weed Research* **50**, 364–372.

Guisan A & Theurillat JP (2000) Equilibrium modeling of alpine plant distribution: how far can we go? *Phytocoenologia* **30**, 353–384.

Guisan A & Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modeling* **135**, 147–186.

INDEC (2010) Instituto Nacional de Estadísticas y Censos. Available at: http://www.sig.indec.gov.ar/censo2010/(last accessed 10 June 2014).

Julien MH, Storrie A & Mccosker R (2004) Lippia, *Phyla canescens*, an increasing threat to agriculture and the environment. 476–479. In: 14th Australian Weeds Conference (eds Sindel BM & Johnson SB). Charles Sturt University, Wagga Wagga, Australia, 718 pp.

Kawecki TJ & Ebert D (2004) Conceptual issues in local adaptation. *Ecology Letters* **7**, 1225–1241.

Landis JR & Koch GC (1977) The measurement of observer agreement for categorical data. *Biometrics* **33**, 159–174.

Macdonald MJ, Whalley WRD, Julien MH, Sindel BM & Duggin JA (2012) Flood-induce recruitment of the invasive perennial herb *Phyla canescens* (lippia). *Rangeland Journal* **34**, 269–276.

Madeira PT, Hill MP, Dray FA Jr, Coetzee JA, Paterson ID & Tipping PW (2016) Molecular identification of *Azolla* invasions in Africa: the Azolla specialist, *Stenopelmus rufinasus* proves to be an excellent taxonomist. *South African Journal of Botany* **105**, 299–305.

Manchester SJ & Bullock JM (2000) The impact on non-native species on UK biodiversity and the effectiveness of control. *Journal of Applied Ecology* **37**, 845–864.

McClay AS, Crisp MD, Evans HC *et al.* (2004) Centres of origin: do they exist, can we identify them, does it matter? In: *Proceedings of the XI International Symposium on Biological Control of Weeds* (eds JM Cullen, DT Briese, DJ Kriticos, WM Lonsdale, L Morin & JK Scott), 619–620. CSIRO Entomology, Canberra, Australia.

McCullagh P & Nelder JA (1989) *Generalized Linear Models*. Chapman and Hall, London, UK.

Moffat CE, Lalonde RG, Ensing DJ, De Clerck-Floate R, Grosskopf-Lachat G & Pither J (2013) Frequency-dependent host species use by a candidate biological control insect within its native European range. *Biological Control* **67**, 498–508.

Murray JV, Stokes KE & Van Klinken RD (2012) Predicting the potential distribution of a riparian invasive plant: the effects of changing climate, flood regimes and land-use patterns. *Global Change Biology* **18**, 1738–1753.

Novoa A, Kumschick S, Richardson DM, Rouget M & Wilson JRU (2016) Native range size and growth form in Cactaceae predict invasiveness and impact. *NeoBiota* **30**, 75–90.

O'Leary N & Múlgura ME (2011) A taxonomic revision of the genus *Phyla* (Verbenaceae). *Annals of the Missouri Botanical Garden* **98**, 578–596.

Paterson ID, Mangan R, Downie DA *et al.* (2016) Two in one: cryptic species discovered in biological control agent populations using molecular data and crossbreeding experiments. *Ecology and Evolution* **6**, 6139–6150.

Peltzer DA, Ferriss S & Fitzjohn RG (2007) Predicting weed distribution at the landscape scale: using naturalized *Brassica* as a model system. *Journal of Applied Ecology* **45**, 467–475.

R Development Core Team (2015) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Steiner FM, Schlick-Steiner BC, Vanderwal J *et al.* (2008) Combined modelling of distribution and niche in invasion biology: a case study of two invasive *Tetramorium* ant species. *Diversity and Distributions* **14**, 538–545.

Stutz S, Tonello MS, González Sagrario MS, Navarro D & Fontana SL (2014) Historia ambiental de los lagos someros de la llanura Pampeana (Argentina) desde el Holoceno medio: inferencias paleoclimáticas. *Latin*

American Journal of Sedimentology and Basin Analysis **21**, 119–138.

Trethowan PD, Robertson MP & Mcconnachie AJ (2011) Ecological niche modeling of an invasive alien plant and its potential biological control agents. *South African Journal of Botany* **77**, 137–146.

Vitousek PM, D'antonio CM, Loope LL, Rejmanek M & Westbrooks R (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* **21**, 1–16.

Xu CY, Schooler SS & Van Klinken RD (2010a) Effects of clonal integration and light availability on the growth and

physiology of two invasive herbs. *Journal of Ecology* **98**, 833–844.

Xu CY, Julien MH, Fatemi M *et al.* (2010b) Phenotypic divergence during the invasion of *Phyla canescens* in Australia and France: evidence for selection-driven evolution. *Ecology Letters* **13**, 32–44.

Xu CY, Tang SQ, Fatemi M *et al.* (2015) Population structure and genetic diversity of invasive *Phyla canescens*: implications for the evolutionary potential. *Ecosphere* **6**, 162.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA & Smith GM (2009) *Mixed Effects Models and Extension in Ecology with R*. Springer, New York, USA.