

# Invasion of glossy privet (*Ligustrum lucidum*) and native forest loss in the Sierras Chicas of Córdoba, Argentina

Laura E. Hoyos · Gregorio I. Gavier-Pizarro ·  
Tobias Kuemmerle · Enrique H. Bucher ·  
Volker C. Radeloff · Paula A. Tecco

Received: 29 June 2009 / Accepted: 8 February 2010 / Published online: 17 March 2010  
© Springer Science+Business Media B.V. 2010

**Abstract** Glossy privet (*Ligustrum lucidum*) is a tree native to China that successfully invades forests of central Argentina. To fully understand glossy privet's ecological effects on native forest, it is necessary to accurately map the distribution of glossy privet stands and the changes in biodiversity and forest structure of the invaded areas. The objectives of this paper were (1) to map the distribution of glossy privet stands in an area representative of the Sierras Chicas (Córdoba, Argentina) and (2) compare composition, structure and regeneration between glossy privet invaded stands and native forest stands. Using four Landsat TM images (October 2005, March, May and July 2006) we mapped the distribution of a glossy privet-dominated stand using a support vector machine, a non-parametric classifier. We recorded

forest structure variables and tree diversity on 105 field plots. Glossy privet-dominated stands occupied 3,407 ha of the total forested land in the study area (27,758 ha), had an average of 33 glossy privet trees (dbh > 2.5 cm) per plot and the cover of their shrub and herb strata was substantially reduced compared with native forest. Forest regeneration was dominated by glossy privet in native forest stands adjacent to glossy privet-dominated stands. We conclude that in the Sierras Chicas glossy privet has become a widespread invader, changing the patterns of vertical structure, diversity, and regeneration in native forests.

**Keywords** Córdoba · *Ligustrum lucidum* · Argentina · Plant invasions · Biodiversity loss · Landsat · Support vector machines

---

L. E. Hoyos (✉) · P. A. Tecco  
Instituto Multidisciplinario de Biología Vegetal (IMBIV-CONICET) and Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Av. Vélez Sarsfield 299, C.C. 495, 5000 Córdoba, Argentina  
e-mail: laurahoyos@gmail.com

G. I. Gavier-Pizarro · T. Kuemmerle · V. C. Radeloff  
Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA

E. H. Bucher  
Centro de Zoología Aplicada, Universidad Nacional de Córdoba, Rondeau 798, P.O. Box 122, Córdoba, Argentina

## Introduction

Invasions by exotic plants are one of the main causes of the degradation of ecosystems and biodiversity globally (Mack and D'Antonio 1998; Mack et al. 2000; Theoharides and Dukes 2007). Exotic plants can have strong effects on ecosystems by altering the dominant vegetation type (e.g., shrubland to grassland conversions), soil properties, biogeochemical cycles, patterns of herbivory and disturbance regimes (Mack et al. 2000; Brooks et al. 2004). Invading trees in particular cause drastic ecosystem changes (Richardson et al. 1994). For example, the invasion of pine trees has

affected large areas dominated by grasses and shrubs in the southern hemisphere, changing the dominant vegetation type, reducing structural diversity, and modifying vegetation patterns and nutrient cycles (Richardson 1998; Zalba and Villamil 2002). In an increasingly globalized world, both frequency and extent of exotic plant invasions are growing rapidly, thus increasing the need to understand their ecological effects and monitor their spread (Vitousek et al. 1997; Meyerson and Mooney 2007).

As elsewhere, non-native trees cause major ecological and economic problems in Argentina, where they have invaded protected areas in the northwest of the country, as well as remnants of natural Neotropical forests (Grau and Aragón 2000; Zalba and Villamil 2002; Richardson et al. 2008). One of the most widespread invasive trees in central Argentina is the glossy privet (*Ligustrum lucidum* W. T. Aiton), which was imported from China as an ornamental (Ribichich and Protomastro 1998; Montaldo 2000). Glossy privet is an aggressive invader in many other countries as well, including Australia and New Zealand (Cronk and Fuller 1995).

Glossy privet grows fast, reaches heights of up to 17 m, and can thrive under both shaded and full sun conditions (Aragón and Groom 2003). Abundant seed are dispersed by birds, and glossy privet also propagate vegetatively (Aragón and Groom 2003; Aragón and Morales 2003). Because of its shade tolerance, glossy privet can grow in relatively undisturbed native forests. Once it reaches the canopy, glossy privet can outcompete most of the native vegetation by creating conditions of low luminosity that hinders the regeneration of other species, ultimately resulting in glossy privet dominance (Grau and Aragón 2000).

Invasive plant dominance can result in substantial changes in the vertical structure of a stand, with negative consequences for biodiversity. For example in Hawaii, the invasive tree species *Fraxinus uhdei* and *Morella faya* form stands with dense canopy cover that reduce understory light availability, eliminating most species in the lower forest strata (Asner et al. 2008). The changes in forest structure can later result in poor habitat for many native animals (Braithwaite et al. 1989; Schmitz et al. 1997), and provide suitable habitat for new invaders and pests (Boppré et al. 1992).

The ecological impact of an exotic invasive plant is not only a function of the local changes in biodiversity

but also of the extent of the dominated area. Detecting invaded areas and mapping the extent and spatial pattern of invasive plants are first steps towards understanding the underlying mechanisms of invasions and developing effective management strategies (Elton 1958; Mack et al. 2000; Rejmanek and Pitcairn 2002). Remote sensing is a powerful tool to map vegetation communities. Several studies used remote sensing images to map distributions of terrestrial non-native invasive plants, relying either on aerial photographs, high-resolution satellite imagery (e.g., Lonsdale 1993; Lass et al. 2005), or airborne hyperspectral imagery (e.g., Hunt et al. 2003; Noujdina and Ustin 2008; Asner et al. 2008). However, in many places neither high-resolution nor hyperspectral data are available or they may be very costly, limiting their use for monitoring plant invasions across large areas, particularly in developing countries.

Landsat satellite images provide an excellent alternative for mapping the spread of non-native invasive plants at broad scales and at low cost, especially given the increasing availability of the global Landsat archives (Woodcock et al. 2008). With an extent of  $185 \times 185$  km, a spatial resolution of  $30 \times 30$  m, and six bands in the visible, near- and shortwave-infrared domain, plus one thermal band, Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) images have been extensively used for ecosystem monitoring (Goward and Masek 2001; Cohen and Goward 2004). Although the spatial resolution of Landsat is often too coarse to map single species (Hunt et al. 2003; Foody et al. 2005), good results for single-species mapping of invasive plants have been obtained when the species of interest forms patches  $>0.5$  ha and is characterized by a spectral signature that is distinct from the surrounding vegetation (Peterson 2005; Bradley and Mustard 2006).

The objectives of this paper were to (1) map the distribution of glossy privet in the study area and (2) determine the effects of invasion on native forest structure and biodiversity. The presence of large glossy privet-dominated patches in the Sierras Chicas of Córdoba represents an excellent opportunity to study glossy privet's impacts on native biodiversity. Knowledge of the spread of glossy privet and the response of the native vegetation is essential to assess the impact of the invasion and to develop regional monitoring and management plans.

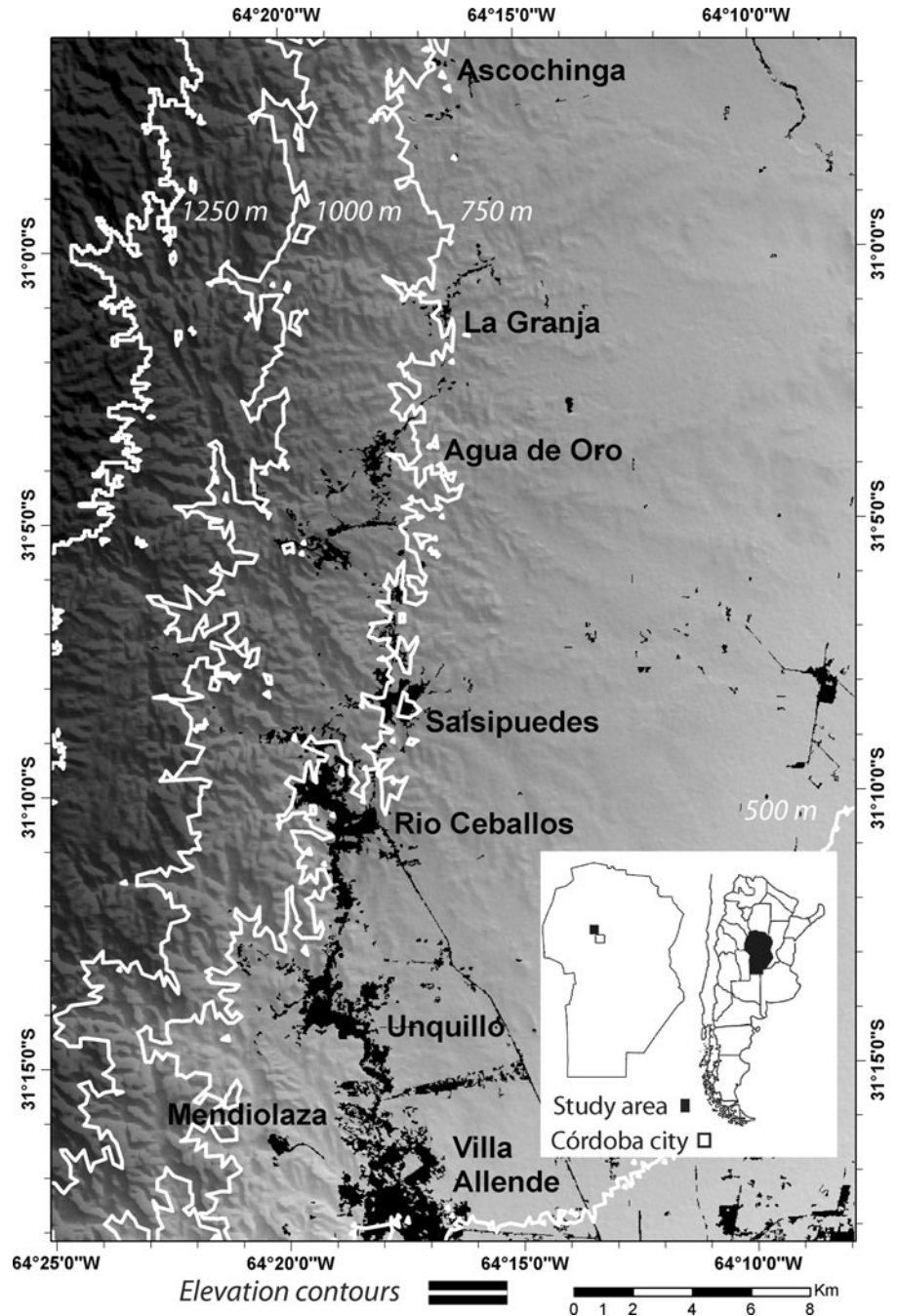
**Methodology**

**Study area**

The study area is located on the eastern slope of the Sierras Chicas of Córdoba, Argentina (North  $-30.943^\circ$ ,

South  $-31.334^\circ$ , West  $64.412$ , East  $64.129$ ) encompassing an area of  $27 \times 41$  km ( $1,130$  km<sup>2</sup>). Altitudes range from 450 m on the eastern plain to 1,350 m on the plateau (Sierras Chicas) in the western part (Fig. 1). Climate is temperate (mean annual temperature of  $18.9^\circ\text{C}$ ) semi-arid with monsoonal rains (average annual

**Fig. 1** Location, topography and urban development of the study area



rainfall is 949 mm; Capitanelli 1979; Gavier and Bucher 2004). The natural vegetation is stratified into four vegetation zones: Llanura (plains below 750 m, dominated by *Aspidosperma quebracho-blanco*, *Prosopis* spp. and *Acacia* spp. forests), Serrano forest (sierras between 1,200 and 700 m, dominated by *Lithraea molleoides* and *Fagara coco* forest), shrubland (between 1,100 and 1,000 m) and grassland (usually above 1,000 m; Luti et al. 1979; Zak and Cabido 2002; Gavier and Bucher 2004).

Land use, predominantly cattle grazing, open mining and extensive logging, have substantially altered natural vegetation communities. Current Deforestation rates between 1970 and 1997 are high (2.8% per year) and forest fragmentation is increasing while the remaining forests are under pressure from grazing, selective logging, fire, and non-native invasive plants (Gavier and Bucher 2004). Urbanization has accelerated since 1970 particularly in forested valleys as people move closer to natural amenities (Zak and Cabido 2002; Gavier and Bucher 2004; Fig. 1). Glossy privet is a widespread invader in the Sierras Chicas of this region, where it was introduced as an ornamental tree around 1900 (Rio and Achaval 1904). It has invaded particularly forested sites resulting in dense stands (Gavier and Bucher 2004).

#### Plant composition, stand structure, and tree regeneration in glossy privet-dominated stands and in native forest stands

We measured stand composition and structure in 105 10 × 10 m field plots (Hays et al. 1981) located in glossy privet-dominated stands (52 plots), native forests (14 plots) (less than 100 m from a glossy privet stand), and native forests far from the invaded areas (39 plots) (more than 200 m away from glossy privet stands). We recorded the number of individuals and diameter at breast height (dbh) for all native and exotic woody species with ≥2.5 cm of dbh in each plot. We also recorded the number of dead standing native trees and the dbh (≥2.5 cm) in each plot. Forest regeneration was estimated by counting the number of individuals of native and exotic woody species with a dbh < 2.5 cm (Sutherland 1996). In the case of privet, no distinction was made between new sapling and vegetative stolons. The basal area of the dominant native and exotic species was estimated following Hays et al. (1981). Plant data were stratified into three

vertical strata: herbaceous (<1 m height), shrubby (1–3 m), and canopy (>3 m). The vegetation cover (%) of each stratum was estimated along 15 m long transects located diagonally in each plot (Hays et al. 1981). The percentages of glossy privet and native tree cover were estimated separately in addition to general canopy cover.

#### Distribution of glossy privet-dominated stands

To map the distribution of glossy privet-dominated stands in the study area, we obtained four Landsat TM images recorded on October 10th 2005, and March 12th, May 15th and July 19th 2006 from the United States Geological Survey Earth Resources Observation and Science data center (USGS EROS) (<http://edc.usgs.gov>). The USGS corrected the images radiometrically (processing level L1T, system correction and conversion to absolute radiance using standard calibration parameters), and orthorectified them to the UTM/WGS 1984 reference system (for details see [http://landsat.usgs.gov/Landsat\\_Processing\\_Details.php](http://landsat.usgs.gov/Landsat_Processing_Details.php)). The positional accuracy of all images was below 0.5 pixel (15 m). We combined the six multispectral bands of each of the four images into a single multitemporal stack with 24 bands that was subset to the extent of the study area. We included bands 1–5 and 7 of each Landsat TM image, but did not use the thermal band (band 6) due to its coarser spatial resolution. Including four images from spring to winter captured important differences in phenology (Dymond et al. 2002; Kuemmerle et al. 2008), because glossy privet is an evergreen plant while the native trees are semi-deciduous.

Based on the satellite imagery, we mapped four land-cover classes: (1) glossy privet-dominated stands in 2006 ('Privet 2006'); (2) native forest-dominated areas ('Native forest'); (3) urban areas ('Urban'); and (4) all other cover types ('Other', accounting mainly for grasslands, shrubs, cropland and water). Training areas for 'Urban' and 'Other' were digitized on the raw Landsat TM/ETM+ images. 'Privet 2006' and 'Native forest' were digitized based on field trips taken during the summers of 2003 and 2004, and October, 2007. To guide the visual interpretation of the Landsat images, we calculated the Normalized Difference Vegetation Index (NDVI) for each image. This index, a normalized quotient of infrared and red bands of Landsat images, has been successfully used

to detect areas invaded by exotics (Bradley and Mustard 2006). Glossy privet-dominated stands differ substantially in structural and physical characteristics from native forest stands. Privet canopies are more dense and close, resulting in higher absorption in the visible domain and higher reflection in the near-infrared domain and thus a higher NDVI (Hoyos 2007).

In the training data for glossy privet, we included digitized polygons from all large invaded patches in the image, and also samples from smaller patches scattered across the image, that were clearly identifiable as glossy privet in accompanying Quickbird images (available in GoogleEarth™, <http://earth.google.com>). For native forest, we included polygons of equivalent areas of Llanura and Serrano forests. Lastly, we digitized polygons for other covers in samples from all parts of the image (e.g., crops from north to south or grass patches in the sierras or the plain areas). For the urban class, the easily recognizable center areas of the four main towns were digitized.

Once training polygons were digitized, a random sample of 400 locations (pixels) for each class was selected from the polygons. These random samples were used to train a support vector machine (SVM) classifier. SVMs are a non-parametric approach that separate classes by fitting a separating hyperplane between two classes in the multidimensional feature space (in our case the 24 bands of the four Landsat images) based on training samples (Huang et al. 2002; Foody and Mathur 2004). The hyperplane that best discriminates two classes maximizes the distance between the hyperplane and the closest training samples (i.e., the support vectors, Burges 1998; Pal and Mather 2005). Thus, rather than describing statistical characteristics of classes, SVMs use only training samples that describe class boundaries (Foody and Mathur 2004). When classes are linearly inseparable, a kernel function transforms training data into a higher dimensional space where a separating linear hyperplane is fitted (Huang et al. 2002; Pal and Mather 2005). Kernel functions thus allow SVMs to handle complex multimodal class distributions and make SVMs well-suited for multi-temporal classifications (Kuemmerle et al. 2008).

Support vector machines were originally designed for binary classifications, but in land cover classification, more than two classes are usually mapped. We used a one-against-one strategy, in which SMVs were

trained for all possible class pairs and every classifier assigns a pixel to one of the two classes. Final class assignment was based on a max-wins voting strategy (i.e., the class that has been assigned most often across all binary classification runs, Vapnik 1995). Running the SVM to classify satellite images requires setting two parameters: the error penalty of misclassified training data ( $C$ ) and the width of the Gaussian kernel function used ( $\gamma$ ). To find suitable parameter combinations, we systematically tested a wide range of  $\gamma$  (0.1–1,000) and  $C$  (0.1–1,000) and compared them based on cross-validation errors (Janz et al. 2007, Kuemmerle et al. 2008).

Once optimal parameters were found, we used the resulting SVM to classify the image stack resulting in a map of glossy privet in 2006 for the study area. For the final map of glossy privet, all patches of any class smaller than 4 pixels (using a 4-neighbor rule) were eliminated by merging them into the largest neighboring patch. We used 153 field plots randomly located and independent from the training data, to validate the classification result for glossy privet stands (110) and native forests (43).

The results for the urban and other classes were validated with 45 and 132 random points respectively using Quickbird images (available in GoogleEarth™, <http://earth.google.com>). To quantify the classification accuracy, we calculated a confusion matrix, and user's and producer's accuracy (Congalton 1991; Foody 2002).

### Statistical analyses

In the first part of our analysis, we compared glossy dominated stands with adjacent native forests. We tested for differences in mean sapling and adult densities, mean dbh, and mean basal area of the species for the privet stands and the adjacent native forest dominated stands with a Mann–Whitney test (Sokal and Rohlf 1979). Significance of the differences in vegetation cover of the three vertical strata between the glossy privet invaded stands and the adjacent native forest dominated stands was tested with a Kruskal–Wallis test (Sokal and Rohlf 1979).

Second, we used a detrended correspondence analysis (DCA; Hill and Gauch 1980) to relate forest structure and composition variables described in Table 1, to different levels of glossy privet invasion. Spearman's correlation tests were used to assess

**Table 1** Variables included in the DCA ordination analysis

Variables	Definition
Specie richness	Number of different species per 100 m <sup>2</sup>
Index of Shannon	Shannon diversity index per 100 m <sup>2</sup>
Glossy privet individuals	Number of adult glossy privets ( <i>Ligustrum lucidum</i> ) per 100 m <sup>2</sup>
Molle individuals	Number of adult molles ( <i>Lithraea molleoides</i> ) per 100 m <sup>2</sup>
Other exotic species	Number of adult individuals of exotic species (except privet) per 100 m <sup>2</sup>
Other native species	Number of adult native arborous individuals (except molle) per 100 m <sup>2</sup>
Dead native species	Number of dead native arborous individuals per 100 m <sup>2</sup>
Dbh of glossy privet	Mean dbh (cm) of adult glossy privet ( <i>L. lucidum</i> ) per 100 m <sup>2</sup>
Dbh of molle	Mean dbh (cm) of adult molle ( <i>L. molleoides</i> ) per 100 m <sup>2</sup>
Dbh of dead native species	Mean dbh (cm) of adult dead native arborous individuals per 100 m <sup>2</sup>
Glossy privet regeneration	Number of glossy privet individuals ( <i>L. lucidum</i> ) smaller than 2.5 cm dbh per 100 m <sup>2</sup>
Molle regeneration	Number of molle individuals ( <i>L. molleoides</i> ) smaller than 2.5 cm dbh per 100 m <sup>2</sup>

which of the variables were most strongly related to the first two ordination axes. We included the 105 plots sampled in glossy privet-dominated stands, adjacent native forest dominated stands, and native forest stands far from invaded areas to represent the full gradient in the level of invasion.

In order to understand the importance of forest regeneration in the invasion process, two additional DCAs were carried out including the 52 plots located in the glossy privet-dominated stands and the 14 plots located in adjacent native forest dominated stands. We compared the ordination of plots in multivariate space in two DCA analyses, the first one did not include the variable number of individuals of glossy privet and *Lithraea molleoides* (molle) smaller than 2.5 cm dbh, and a second DCA that included individuals smaller than 2.5 cm dbh (Table 1).

## Results

Plant composition, stand structure and tree regeneration in glossy privet-dominated and adjacent native forest stands

### Stand composition

We counted 2,201 woody species individuals >2.5 cm dbh, 16,632 individuals <2.5 cm dbh, and 460 snags of native trees, most of them (70%) in the glossy privet stands. A total of 29 woody species (i.e.,

10 exotic species and 19 native species) were identified in the field plots (Table 2). The number of individuals was highly variable among species and forest types (Table 2).

Glossy privet represented almost 77% of the woody plants >2.5 cm dbh recorded in the study area. As expected, glossy privet was the most abundant species and represented the largest basal area in the glossy privet-dominated stands, whereas the native species *Lithraea molleoides* (molle), *Celtis chichape* (tala), and *Acacia praecox* (garabato) were the most abundant species and represented the largest basal area in the adjacent native forests (Mann–Whitney  $P < 0.05$ ; Table 2).

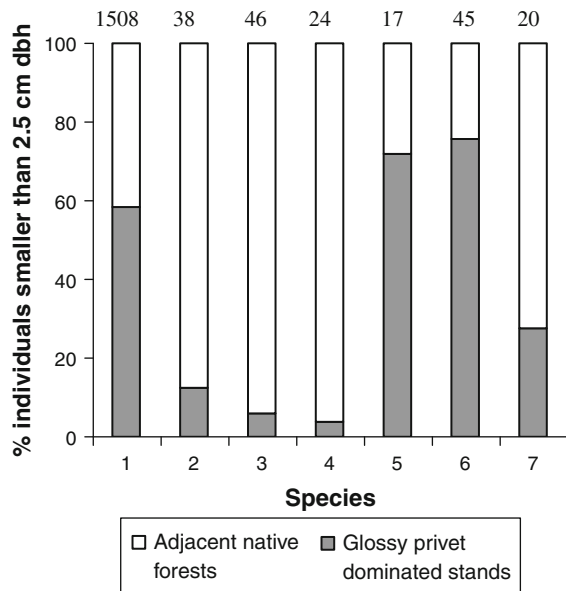
We found consistent differences in species composition and the abundance of individuals <2.5 cm dbh between glossy privet-dominated stands and adjacent native forest stands (Fig. 2). However, the number of glossy privet individuals <2.5 cm dbh did not differ between the glossy privet-dominated stands (58.5%) and the adjacent native forest stands (41.4%). The numbers of native individuals both larger and smaller than 2.5 cm dbh such as *Lithraea molleoides*, *Celtis chichape* and *Acacia praecox* were higher in the adjacent native forest stands than in the glossy privet-dominated stands (Mann–Whitney  $P < 0.05$ ). The mean dbh of the *Celtis chichape* and of dead standing native trees was higher in the glossy privet-dominated stands (11.8 and 8.25 cm, respectively) than in the adjacent native forest (8.43 and 6.37 cm; Mann–Whitney  $P < 0.05$ ; Table 2).

**Table 2** List of woody species sampled in the glossy privet-dominated stands and the native forest dominated stands in the Sierras Chicas of Córdoba

	Regeneration		<i>P</i>	Adults		<i>P</i>
	Glossy privet-dominated stands	Adjacent native forests		Glossy privet-dominated stands	Adjacent native forests	
Exotic species						
<i>Acer negundo</i>	–	–	–	0 (1)	0 (0)	0.6038
<i>Gleditsia triacanthos</i>	4 (215)	8 (107)	0.011	0 (7)	0 (4)	0.587
<i>Laurus nobilis</i>	0 (3)	0 (0)	0.604	0 (1)	0 (0)	0.6038
<i>Ligustrum lucidum</i>	170 (8,835)	447 (6,253)	0.500	33 (1,711)	10 (143)	<0.0001
<i>Manihot flabellifolia</i>	5 (274)	8 (106)	0.040	0 (23)	0 (3)	0.8464
<i>Melia azedarach</i>	3 (140)	0 (6)	0.056	0 (19)	0 (2)	0.7771
<i>Morus</i> sp.	–	–	–	0 (14)	0 (0)	0.0622
<i>Porlieria chilensis</i>	0 (2)	3 (41)	0.000			
<i>Robinia pseudo-acacia</i>	–	–	–	0	0 (2)	0.0539
<i>Ulmus pumilla</i>	–	–	–	0 (4)	0 (0)	0.6038
Total no. of exotic individuals	9,469	6,513		1,780	154	
Native species						
<i>Acacia aramo</i>	–	–	–	0 (1)	0 (2)	0.303
<i>Acacia caven</i>	0 (5)	0 (2)	0.835	0 (0)	0 (5)	0.0007
<i>Acacia praecox</i>	0 (16)	31 (436)	<0.0001	0 (5)	2 (33)	<0.0001
<i>Bauhinia forficata</i> <sup>a</sup>	1 (26)	0 (0)	0.604	0 (23)	0 (0)	0.6038
<i>Bougainvillea stipitata</i>	0 (2)	1 (10)	0.046	0 (3)	1 (11)	0.0002
<i>Caesalpinia gilliesii</i>	0 (0)	0 (5)	0.054	0 (0)	0 (2)	0.0539
<i>Celtis chichape</i>	0 (1)	1 (16)	0.001	0 (14)	2 (22)	0.0003
<i>Cereus forbesii</i>	–	–	–	0 (0)	0 (1)	0.0539
<i>Condalia montana</i>	0 (9)	2 (30)	<0.0001	0 (4)	1 (19)	0.0003
<i>Fagara coco</i>	0 (1)	1 (11)	0.001	0 (2)	0 (2)	0.1493
<i>Geoffroea decorticans</i>	–	–	–	0 (0)	0 (1)	0.0539
<i>Jodina rhombifolia</i>	0 (0)	0 (1)	0.054	–	–	–
<i>Kageneckia lanceolata</i>	–	–	–	0 (1)	1 (11)	0.303
<i>Lithraea molleoides</i>	0 (3)	2 (21)	<0.0001	1 (30)	2 (27)	0.0008
<i>Prosopis nigra</i>	0 (0)	1 (11)	0.054	0 (0)	0 (3)	0.006
<i>Ruprechtia apetala</i>	0 (0)	3 (36)	<0.0001	0 (2)	2 (30)	<0.0001
<i>Salix alba</i>	–	–	–	0 (9)	0 (0)	0.6038
<i>Schinus areira</i> <sup>a</sup>	–	–	–	0 (0)	0 (1)	0.0539
<i>Sebastiania commersoniana</i>	0 (8)	0 (0)	0.604	0 (2)	0 (1)	0.6019
Total no. of native individuals	71	579		96	171	
Total no. of native and exotic individuals	9,540	7,092		1,876	325	
Dead native trees	0 (0)	0 (1)	0.054	7 (338)	9 (122)	0.4086

Mean and absolute number (between parentheses) of adults (dbh > 2.5 cm) and regeneration (dbh < 2.5 cm) are provided for each species. Mann–Whitney, *P* < 0.05

<sup>a</sup> South of Brazil, Uruguay and North of Argentina



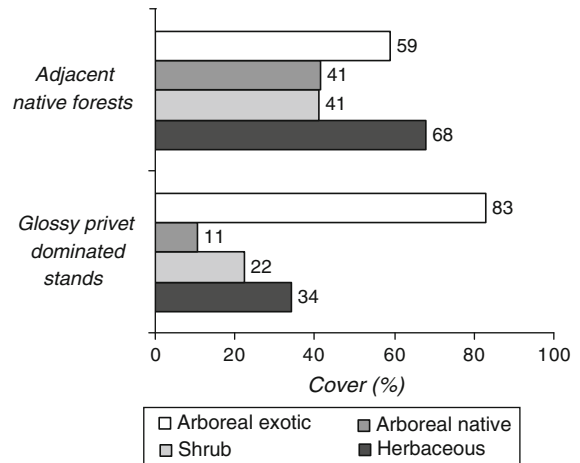
**Fig. 2** Percentage of different tree species <2.5 cm dbh in glossy privet-dominated stands and adjacent native forests. (1) *Ligustrum lucidum*, (2) *Manihot flabellifolia*, (3) Other exotic tree species, (4) *Litsea molleoides*, (5) *Celtis chichape*, (6) *Acacia praecox* and (7) Other native tree species. The numbers on the top represent the abundance of each species

### Vertical structure

The vertical structure of the vegetation in glossy privet-dominated stands and adjacent native forest dominated stands was also different (Fig. 3). Cover of the herbaceous and shrubby strata was substantially lower in the glossy privet-dominated stands than in the adjacent native forests (Mann–Whitney,  $P = 0.005$  and  $P = 0.014$ , respectively; Fig. 3). The percentage of glossy privet canopy cover was higher (83%) than the canopy cover of native species (10%) in the glossy privet-dominated stands (Kruskal–Wallis,  $P < 0.0001$ ). Interestingly, the percentage of glossy privet tree canopy cover was also higher in the adjacent native forests (59%) than the canopy cover by native species (41%) (Kruskal–Wallis,  $P < 0.0001$ ).

### Variation in forest structure and composition along a gradient of glossy privet invasion

Forest stand characteristics separated the field plots in three groups representing different glossy privet invasion conditions. The first axis of the DCA analysis explained 48% of the total variability, and represented



**Fig. 3** Vertical structure of the glossy privet-dominated stands and adjacent native forests. The bars represent the percentages of cover of the herbaceous, shrubby, and canopy strata for both types of forest. In the case of the canopy, bars of native and exotic cover are provided separately. Percentage of cover is indicated at the bar extremes

a gradient from plots with a large number of adult glossy privet individuals and dead native trees, to plots with a large diversity and large numbers of native trees, particularly of molle (Fig. 4).

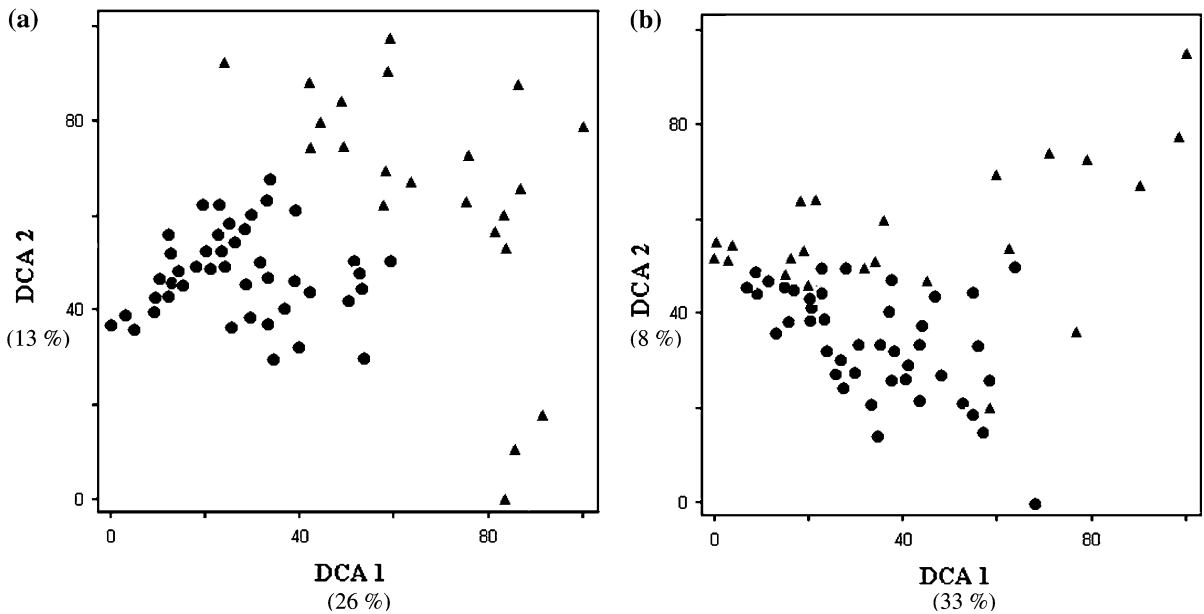
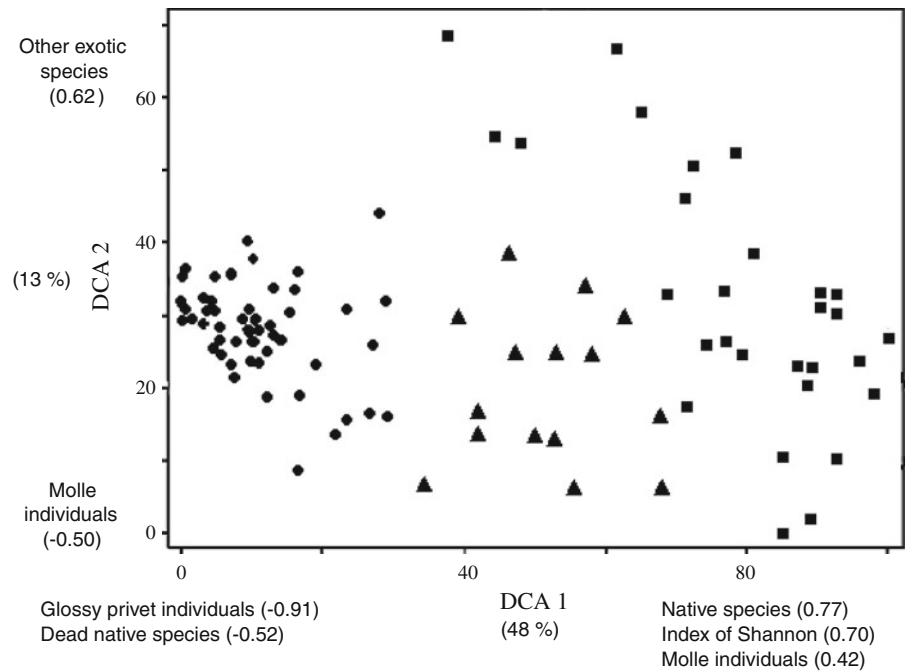
Most plots of glossy privet-dominated stands were part of a cluster in the DCA ordination that represented homogeneous forest structure characteristics, with large numbers of glossy privet adult individuals and dead standing native trees. A few glossy privet-dominated plots represented stands with a lower density of glossy privet adults. The native forest dominated stands formed two different groups. The plots located in native forests adjacent to glossy privet-dominated stands were in an intermediate condition between glossy privet-dominated stands and native forests afar from glossy privet stands, with a variable number of individual glossy privet growing intermixed with native trees. The plots located in native forests afar from glossy privet-dominated stands occupied the extreme of the gradient with large numbers and high diversity of native trees, and with an especially large number of molle (Fig. 4).

### Tree regeneration and glossy privet invasion conditions

When forest regeneration was not considered as an ordination variable, plots located in glossy privet-



**Fig. 4** Structure and composition of glossy privet-dominated stands (*filled circle*), adjacent native forest (*filled triangle*) and native forests dominated stands afar from invaded areas (*filled square*). The variables most strongly correlated to ordination axes are listed with their respective correlation coefficient in brackets (Spearman Rank Correlation,  $P < 0.05$ )



**Fig. 5** Differences in forest structure and composition of glossy privet-dominated stands (*filled circle*) and adjacent native forests stands (*filled triangle*); **a** without considering

dominated stands were clearly separated from plots located in adjacent native forest dominated areas in the DCA ordination. Plots in glossy privet-dominated stands formed a cluster associated with large numbers of glossy privet individuals in axes 1 and 2

regeneration of glossy privet and molle, and **b** including regeneration of glossy privet and molle

of the ordination. The plots located in adjacent native forests were more widely distributed along both axes, but always positively associated with the number and diversity of native trees (Fig. 5a; Table 3).

**Table 3** The variables most strongly correlated to ordination axes with their respective correlation coefficient (Spearman rank correlation, \*  $P < 0.05$ )

Variables	Without considering regeneration of glossy privet and molle		Including regeneration of glossy privet and molle	
	DCA 1	DCA 2	DCA 1	DCA 2
Species richness	0.63*	0.35*	0.19	0.62*
Index of Shannon	0.73*	0.66*	0.33*	0.63*
Glossy privet individuals	-0.73*	-0.73*	-0.34*	-0.57*
Molle individuals	0.67*	-0.06	0.20	0.61*
Native species	0.75*	0.55*	0.24*	0.72*
Dead native species	0.12	-0.04	0.29*	-0.05
Dbh glossy privet	0.27	0.29*	0.35*	-0.02
Dbh molle	0.53*	-0.44*	-0.11	0.42*
Dbh of dead native species	-0.25	0.08	-0.07	-0.30*
Saplings of privet	-	-	-0.97*	0.28*
Saplings of molle	-	-	0.39*	0.54*

However, when the number of trees  $<2.5$  cm dbh was included as an ordination variable, the ordination of plots located in native forests adjacent to glossy privet became more similar to plots located in glossy privet-dominated areas (Fig. 5b; Table 3). Along DCA axis 1, most of the plots located in adjacent native forest dominated stands tended to be associated with a large number of glossy privet individuals  $<2.5$  cm dbh, representing forest regeneration similar to the plots located in the glossy privet-dominated stands.

#### Distribution of glossy privet-dominated stands

Glossy privet was widespread in the study area constituting one of the main land cover types, with an area of 3,407 ha (i.e., 12% of the total forested area of 27,758 ha). The spatial distribution of glossy privet-dominated stands was not homogeneous, with most stands located either close to urban areas or to native forests (Fig. 6).

Most of the glossy privet-dominated stands were located in the southern half of the study area, especially near the towns of Salsipuedes and Rio Ceballos, and west of the road connecting the towns of Rio Ceballos and Unquillo, on slopes dominated by native forest stands. The distribution of glossy privet stand sizes was highly variable, but glossy privet formed large stands. The largest glossy privet stand was located between Rio Ceballos and Salsipuedes (262 ha). Two other large stands (173 and

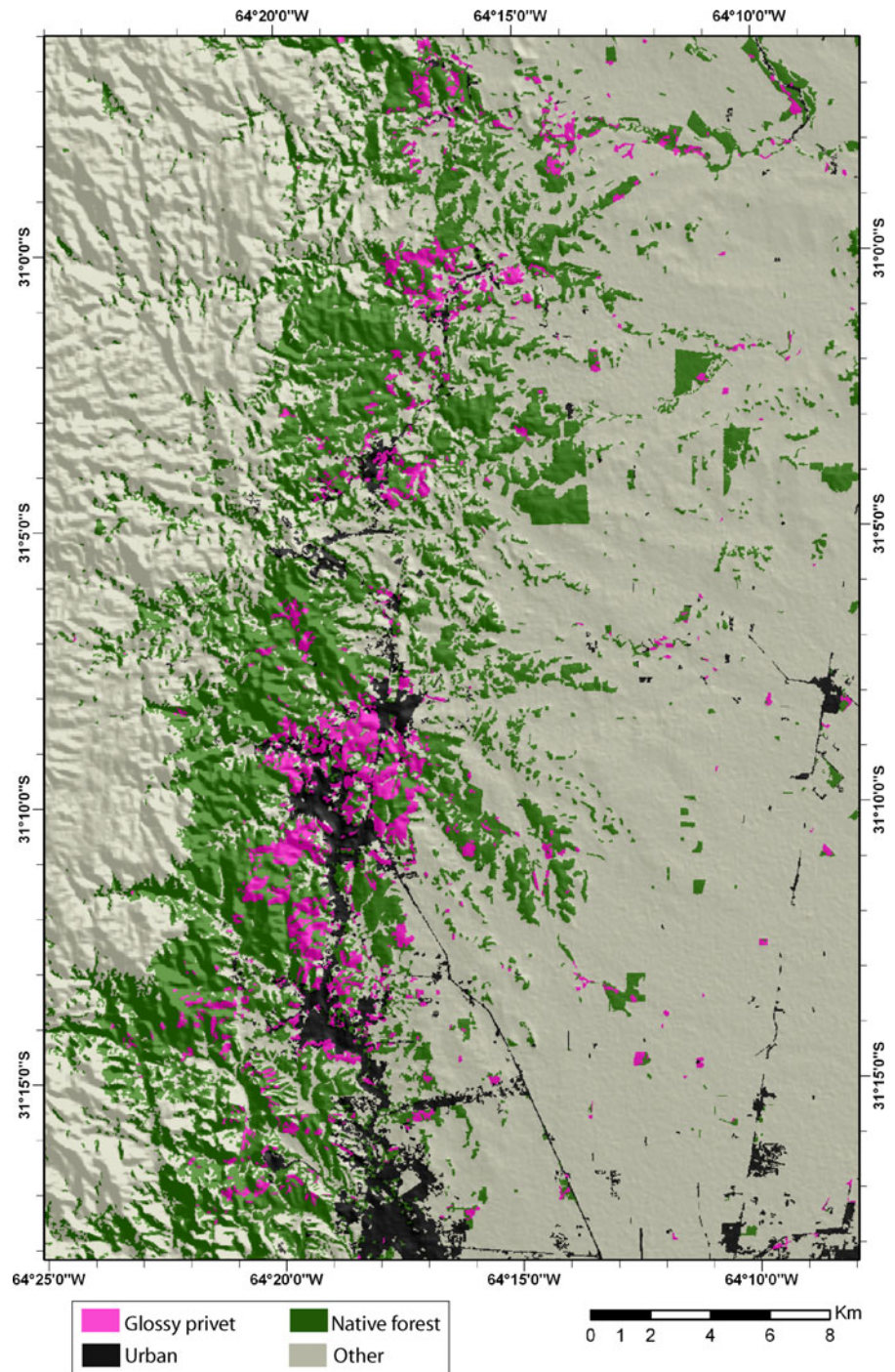
177 ha) were located east and south of the town of Rio Ceballos. Two more glossy privet stands around 100 ha were located south of Salsipuedes. The five stands larger than 100 ha contained 24% of the total glossy privet-dominated area. In the northern part of the study area, there were only a few stands larger than 50 ha; all of them located close to urban areas (Fig. 6).

The classification of the Landsat TM images stacked with SVM, differentiated glossy privet areas very well from other natural and human land cover types. The 2006 classification was highly accurate, particularly for glossy privet-dominated stands (user's accuracy of 91.7%, producer's accuracy of 81.7%). The overall accuracy for the 2006 map was 89% (Table 4).

#### Discussion

In the study area, the invasion of glossy privet (*Ligustrum lucidum*) has reached a critical level. Glossy privet forms large, almost single-species stands that have become one of the main vegetation cover types, similar to other areas in Australia and northern Argentina (Swarbrick et al. 1999; Grau et al. 2008). The glossy privet-dominated stands are very different in terms of their vertical structure and composition from native forests. The cover loss in both the herbaceous and the shrubby strata

**Fig. 6** Distribution of glossy privet-dominated stands, native forest, urban areas, and other landcover in the study area in 2006



represented a substantial simplification of the vertical structure of glossy privet-dominated stands compared to native forest. The glossy privet invasion is a dynamic process. Native forest dominated stands adjacent to glossy privet-dominated stands showed a

substantial invasion of glossy privet, with occasional adult glossy privet trees reaching the canopy, and tree regeneration being dominated by glossy privet.

In the study area, glossy privet seems to follow two modes of invasion. The first is the invasion of

**Table 4** Accuracy assessment (confusion matrix and accuracy percent) for the classification of Landsat images for the study area in four classes

	Reference data	Classification data					
		Glossy privet	Native forest	Other	Urban	Total	Producers accuracy
Glossy privet	89	13	3	4	109	81.7	
Native forest	3	34	5	2	44	77.3	
Other	0	1	131	1	133	98.5	
Urban	0	0	0	46	46	100.0	
Total	92	48	139	53	332		
Overall classification accuracy = 89%	User's accuracy	96.7	70.8	94.2	86.8		

native forest, where glossy privet can spread due to its shade-tolerance. We often found glossy privet in native forests adjacent to invaded stands (both as scattered adult trees and glossy privet regeneration) and we found many dead standing native trees in glossy privet dominated stands.

Field data indicated the suppression of native forest regeneration in glossy privet stands. The regeneration of native tree species in the glossy privet invaded areas was very scarce. Optimal conditions for molle seed germination (i.e., complete sun exposure and moderate humidity, Bianco 1989; Marco and Páez 2000) are not found under the dense evergreen canopy of glossy privet stands, which cast strong shade all year long. On the other hand, glossy privet regeneration was very high both under its own canopy and in adjacent native forests, because glossy privet can germinate and survive in a broad range of ecological conditions (Aragón and Groom 2003; Tecco et al. 2007).

Most of the native trees under the glossy privet canopy were dead. Only large individuals of molle (taller than the glossy privet canopy) were able to survive, similar to what was observed in Australia where only tall individuals of *Eucalyptus* spp. remained in glossy privet-dominated stands (Montaldo 1993; Swarbrick et al. 1999; Primack and Ros 2002).

The second invasion mode is the rapid spread of glossy privet in cleared areas where it outcompetes native early-successional species. Many of the glossy privet-dominated stands were located in areas that were cleared or selectively logged between 1940 and 1960 to support urbanization plans that were later abandoned (Gavier 2002). The relatively even-aged population structure of some glossy privet-dominated stands may thus be the result of fast colonization of cleared native forest stands. Soil disturbances favor the establishment of glossy privet, limit competition

from other tree species and increase nutrient availability (Buchanan 1989).

However, our results show that under both invasion modes glossy privet stands limit native plant biodiversity and prevent native forest regeneration. The elimination of the majority of the native plant cover, and particularly of arboreal species, in glossy privet-dominated stands, is likely due to the strong shade cast by glossy privet, which constrains the regeneration and growth of other species (Grau and Aragón 2000; Merriam and Fiel 2002). Furthermore, glossy privet grows taller than native trees outcompeting them in the competition for light (Swarbrick et al. 1999).

The widespread distribution of glossy privet in the study area can be related to its bird distributed seed. Glossy privet is a prolific fleshy fruit producer, and its seeds are widely dispersed by common native birds, such as *Turdus* spp. (Montaldo 1993, 2000; Aragón 2000). Glossy privet produces fruit during the cold season while most natives plants fructify in the warm season, which increases the likelihood that glossy privet seeds are consumed and dispersed by birds (Grau and Aragón 2000; Gurvich et al. 2005; Tecco et al. 2006). Thus, bird dispersion of seeds can result in a high rate of propagule spread into native forests throughout the study area.

A combination of bird dispersion and ecological conditions may explain the higher rate of glossy privet invasion into forests compared to grasslands and shrublands. Glossy privet can germinate and survive in a broad range of environmental conditions (Aragon and Groom 2003) and its consumption by birds and ability to germinate from intact fruit gives glossy privet a capacity of recruitment in both new and invaded patches. However, the establishment of glossy privet in open fields is constrained by low germination success and high seedling mortality, but

the invasibility of open sites may change after a few shrubs and trees are established and can attract dispersers and provide protection (Aragón and Groom 2003). Another factor may be that in our study area, grasslands and shrublands are located at higher altitude. Dry conditions and more frequent wind at higher altitudes cause more fires, which may limit glossy privet. Grazing may also prevent glossy privet establishment and growth.

In terms of our approach, the classification of Landsat TM images with a SVM successfully mapped glossy privet dominated stands. The 96% detection accuracy for glossy privet-dominated stands was comparable to the 97% accuracy obtained for mapping invasive grasses with a hyperspectral sensor (Lass et al. 2005) and superior to the 65–74% accuracy obtained for mapping invading gramineae with Landsat TM images (Bradley and Mustard 2006). However, we also noted some limitations of Landsat TM imagery for glossy privet mapping.

The spatial and spectral resolution of the Landsat TM sensor did not allow us to detect mixed stands of glossy privet and native trees. The areas of adjacent native forest where glossy privet individuals are mixed with native trees were classified as native forests, even when the cover of glossy privet in the canopy was larger than that of native trees. Based on our field plots, glossy privet canopy cover had to be larger than 60% for an area to be classified as glossy privet. In other words, our classification mapped the areas that were fully dominated by glossy privet well, but underestimated the total amount of glossy privet distributed in the area.

Our results have important conservation and management implications. Our field data highlighted that glossy privet is spreading very fast in the study area. The preference of glossy privet for more shaded and humid conditions (Swarbrick et al. 1999) overlaps with the areas where the native forests in the sierras achieve the largest canopy cover (Zak and Cabido 2002), thus increasing the likelihood of negative impacts on native forest of special conservation value. In many native forests, tree regeneration is completely dominated by glossy privet, and these seedlings and saplings will potentially reach the canopy and kill native vegetation with strong shade. The process will accelerate if native forests are also stressed by selective logging, clearcuts, overgrazing, or urban development (Gavier and Bucher 2004). And bird dispersal of seeds fosters the invasion of

glossy privet even into those native forests that are protected from human disturbances by either topography, or land use regulations.

The negative ecological consequences of conversion of native forest stands into glossy privet-dominated stands are likely substantial. Our data show that the biodiversity of native trees declines and that vertical structure is much less complex in glossy privet-dominated stands. Birds that feed heavily on glossy privet seed will potentially be favored over other species. Other potential consequences may include changes in nutrient cycling, soil properties, and disturbance regimes, but examining these effects was beyond the scope of our study.

In summary, glossy privet was already widespread, and will likely become an even larger threat to the forest ecosystem of the Sierras Chicas de Cordoba of Central Argentina. Limiting the spread of glossy privet and reducing its current extent should be a management priority for municipalities, government agencies, and conservation groups. Maps of glossy privet-dominated stands obtained by Landsat TM images, like the ones presented in our study can help to prioritize areas for management, and are necessary for the entire current range of glossy privet in Argentina.

**Acknowledgments** We thank A. Cingolani for valuable comments and suggestions on previous versions of the manuscript. C. Blumzak provided valuable assistance in the field. S. Benavidez generously provided field plot data for native forests. S. Schmidt, M. Hoyos and T. Albright greatly improved the English. We thank also two anonymous reviewers for the helpful comments during the reviewing process which substantially improved the manuscript. We gratefully acknowledge support from a Tinker-Nave Short Term Field Research Grant of the Latin American, Caribbean and Iberian Studies Program (University of Wisconsin-Madison) and the Fulbright/Organization of American States Fellowship to G. Gavier-Pizarro, from the Master in Wildlife Management Program (Maestría en Manejo de Vida Silvestre) of the National University of Córdoba to L. Hoyos, and a Fedor Lynen Research Fellowship by the Alexander von Humboldt Foundation to T. Kuemmerle. We would also like to thank A. Rabe, S. van der Linden, and P. Hostert for sharing the image SVM software and for helpful discussions.

## References

- Aragón R (2000) Especies exóticas como recurso para las aves en bosques secundarios de las yungas. In: Grau HR, Aragón R (eds) Ecología de árboles exóticos en las yungas Argentinas. LIEY, Tucumán

- Aragón R, Groom M (2003) Invasion by *Ligustrum lucidum* (Oleaceae) in NW Argentina: early stage characteristics in different habitat types. *Rev Biol Trop* 51:59–70
- Aragón R, Morales JM (2003) Species composition and invasion in NW Argentinian secondary forest: effects of land use history, environment and landscape. *J Veg Sci* 14:195–204
- Asner GP, Jones MO, Martin RE, Knapp DE, Hughes RF (2008) Remote sensing of native and invasive species in Hawaiian forests. *Remote Sens Environ* 112:1912–1926
- Bianco SE (1989) Estudio sobre la germinación de *Lithraea ternifolia* (GILL) BARKLEY, ROM y descripción de frutos, semillas y plántulas. Tesina. Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba
- Boppré M, Biller A, Fischer OW, Hartmann T (1992) The non-nutritional relationship of *Zonocerus* (Orthoptera) to *Chromolaena* (Asteraceae). In: Menken SBJ, Visser JH, Harrewijn P (eds) Proceedings of the 8th international symposium insect-plant relationships. Kluwer Academic, Dordrecht, pp 89–90
- Bradley BA, Mustard JF (2006) Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecol Appl* 16:1132–1147
- Braithwaite RW, Lonsdale WA, Estbergs JA (1989) Alien vegetation and native biota in tropical Australia: the spread and impact of *Mimosa pigra*. *Biol Conserv* 48:189–210
- Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. *Bioscience* 54:677–688
- Buchanan RA (1989) Bush regeneration. Department of Technical and Further Education [NSW], Sydney
- Burges CJC (1998) A tutorial on support vector machines for pattern recognition. *Data Min Knowl Discov* 2:121–167
- Capitanelli RG (1979) Clima. In: Vázquez JB, Miatello RA, Roque E (eds) Geografía Física de la Provincia de Córdoba. Buenos Aires, Boldt, pp 45–138
- Cohen WB, Goward SN (2004) Landsat's role in ecological applications of remote sensing. *Bioscience* 54(6):535–545
- Congalton RG (1991) A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sens Environ* 37:35–46
- Cronk QCB, Fuller JL (1995) Plant invaders: the threat to natural ecosystems. Chapman & Hall, London
- Dymond CC, Mladenoff DJ, Radeloff VC (2002) Phenological differences in Tasseled Cap indices improve deciduous forest classification. *Remote Sens Environ* 80:460–472
- Elton CS (1958) The ecology of invasions by animals and plants. Methuen & Co, London
- Foody GM (2002) Status of land cover classification accuracy assessment. *Remote Sens Environ* 80:185–201
- Foody GM, Mathur A (2004) A relative evaluation of multi-class image classification by support vector machines. *IEEE Trans Geosci Remote Sens* 42(6):1335–1343
- Foody GM, Atkinson PM, Gething PW, Ravenhill NA, Kelly CK (2005) Identification of specific tree species in ancient semi-natural woodland from digital aerial sensor imagery. *Ecol Appl* 15:1233–1244
- Gavier G (2002) Deforestación y Fragmentación del Bosque en las Sierras Chicas de Córdoba, Argentina. Tesis de Maestría, Programa de Postgrado en Manejo de Vida Silvestre, Universidad Nacional de Córdoba, Argentina
- Gavier G, Bucher EH (2004) Deforestación de las Sierras Chicas de Córdoba (Argentina) en el período 1970–1997. *Academia Nacional de Ciencias Miscelánea* 101:1–27
- Goward SN, Masek JG (2001) Landsat—30 years and counting. *Remote Sens Environ* 78:1–2
- Grau HR, Aragón R (2000) Árboles Invasores de la Sierra de San Javier, Tucumán Argentina. In: Grau HR, Aragón R (eds) Ecología de árboles exóticas en las yungas Argentinas. LIEY, Tucumán
- Grau HR, Gasparri NI, Aide TM (2008) Balancing food production and nature conservation in the Neotropical dry forests of northern Argentina. *Glob Chang Biol* 14:985–997
- Gurvich DE, Tecco PA, Díaz S (2005) Plant invasion in undisturbed ecosystems: the triggering attribute approach. *J Veg Sci* 16:723–728
- Hays RL, Summers C, Seitz W (1981) Estimating wildlife habitat variables. Biological Services Program, Fish and Wildlife Service, US Department of the Interior
- Hill MO, Gauch HG (1980) Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42:47–58
- Hoyos LE (2007) Evaluación del grado de invasión del siempreverde (*Ligustrum lucidum*) en la Sierras Chicas de Córdoba. Tesis de Maestría, Programa de Postgrado en Manejo de Vida Silvestre, Universidad Nacional de Córdoba, Argentina
- Huang C, Davis LS, Townshend RG (2002) An assessment of support vector machines for land cover classification. *Int J Remote Sens* 23:725–749
- Hunt ER, Everitt JH, Ritchie JC, Moran MS, Booth DT, Anderson GL, Clark PE, Seyfried MS (2003) Applications and research using remote sensing for rangeland management. *Photogramm Eng Remote Sens* 69:675–693
- Janz A, van der Linden S, Waske B, Hostert P (2007) ImageSVM—a user-oriented tool for advanced classification of hyperspectral data using support vector machines. In: Reusen I, Cools J (eds) EARSeL SIG imaging spectroscopy. Bruges, Belgium
- Kuemmerle T, Hostert P, Radeloff VC, van der Linden S, Perzanowski K, Kruhlov I (2008) Cross-border comparison of post-socialist farmland abandonment in the Carpathians. *Ecosystems* 11:614–628
- Lass LW, Prather TS, Glenn NF, Weber KT, Mundt JT, Pettigill JA (2005) Review of remote sensing of invasive weeds and example of the early detection of spotted knapweed (*Centaurea maculosa*) and babysbreath (*Gypsophila paniculata*) with a hyperspectral sensor. *Weed Sci* 53:242–251
- Lonsdale WM (1993) Rates of spread of an invading species—*Mimosa pigra* in Northern Australia. *J Ecol* 81:513–521
- Luti R, Galera MA, Muller N, Berzal N, Nores M, Herrera M, Barrera JC (1979) Vegetación. In: Vázquez JB, Miatello RA, Roqué ME (eds) Geografía Física de la Provincia de Córdoba. Banco de la Provincia de Córdoba, Editorial Boldt

- Mack MC, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. *Tree* 13:195–198
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Marco DE, Páez SA (2000) Invasion of *Gleditsia triacanthos* in *Lithraea ternifolia* montane forest of central Argentina. *Environ Manage* 26:409–419
- Merriam RW, Fiel E (2002) Potential impact of an introduced shrub on native plant diversity and forest regeneration. *Biol Invasions* 4:369–373
- Meyerson LA, Mooney HA (2007) Invasive alien species in an era of globalization. *Front Ecol Environ* 5:199–208
- Montaldo NH (1993) Dispersión por aves y éxito reproductivo de dos especies de *Ligustrum* (Oleaceae) en un relicto de selva subtropical en la Argentina. *Rev Chil Hist Nat* 66:75–85
- Montaldo NH (2000) Reproductive success of bird-dispersed plants in a subtropical forest relict in Argentina. *Rev Chil Hist Nat* 73:511–524
- Noujdina NV, Ustin SL (2008) Mapping downy brome (*Bromus tectorum*) using multivariate AVIRIS data. *Weed Sci* 56:173–179
- Pal M, Mather PM (2005) Support vector machines for classification in remote sensing. *Int J Remote Sens* 26:1007–1011
- Peterson EB (2005) Estimating cover of an invasive grass (*Bromus Tectorum*) using tobit regression and phenology derived from two dates of Landsat Etm Plus Data. *Int J Remote Sens* 26:2491–2507
- Primack RB, Ros J (2002) Introducción a la Biología de la Conservación. Editorial Ariel
- Rejmanek M, Pitcairn MJ (2002) When is eradication of exotic pest plants a realistic goal. In: Veitch CR, Clout MN (eds) Turning the tide: the eradication of invasive species. Occasional Paper of the IUCN Species Survival Commission, IUCN SSC Invasive Species Specialist Group, Gland
- Ribichich AM, Protomastro J (1998) Woody vegetation structure of xeric forest stands under different edaphic site conditions and disturbance histories in the Biosphere Reserve 'Parque Costero del Sur', Argentina. *Plant Ecol* 139:189–201
- Richardson DM (1998) Forestry trees as invasive aliens. *Conserv Biol* 12:18–26
- Richardson DM, Williams PA, Hobbs RJ (1994) Pine Invasion in the Southern Hemisphere: determinants of spread and invadability. *J Biogeogr* 21:511–527
- Richardson DM, van Wilgen B, Nuñez MA (2008) Alien conifer invasions in South America: short fuse burning? *Biol Invasions* 10:573–577
- Rio ME, Achaval L (1904) Geografía de la Provincia de Córdoba. Compañía Sud-Americana de Billetes de Banco, Buenos Aires
- Schmitz DC, Simberloff D, Hofstetter RH, Haller W, Sutton D (1997) The ecological impact of the nonindigenous plants. In: Simberloff D, Schmitz DC, Brown TC (eds) Strangers in paradise: impact and management of nonindigenous species in Florida. Island, Washington, DC, pp 39–61
- Sokal R, Rohlf F (1979) Biometría. Principios y Métodos Estadísticos en la Investigación Biológica, H. Blume Ediciones
- Sutherland WJ (1996) Ecological census techniques: a handbook. Cambridge University Press, Cambridge
- Swarbrick JT, Timmins SM, Bullen KM (1999) The biology of Australian weeds. 36. *Ligustrum lucidum* Aiton and *Ligustrum sinense* Lour. *Plant Prot Q* 14:122–130
- Tecco PA, Gurvich DE, Díaz S, Pérez-Harguindeguy N, Cabido M (2006) Positive interaction between invasive plants: the influence of *Pyracantha angustifolia* on the recruitment of native and exotic woody species. *Austral Ecol* 31:293–300
- Tecco PA, Díaz S, Gurvich DE, Pérez-Harguindeguy N, Cabido M, Bertone GA (2007) Experimental evidence of positive association between exotic woody species: facilitation by *Pyracantha angustifolia* on *Ligustrum lucidum* sapling survival. *Appl Veg Sci* 10:211–218
- Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytol* 176:256–273
- Vapnik V (1995) The nature of statistical learning theory. Springer, New York
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of earth's ecosystems. *Science* 277:494–499
- Woodcock CE, Allen R, Anderson M, Belward A, Bindschadler R, Cohen WB, Gao F, Goward SN, Helder D, Helmer E, Nemani R, Oreopoulos L, Schott J, Thenkabail PS, Vermote EF, Vogelmann J, Wulder MA, Wynne R (2008) Free access to Landsat imagery. *Science* 320:1011
- Zak MR, Cabido M (2002) Spatial patterns of the Chaco vegetation of central Argentina: integration of remote sensing and phytosociology. *Appl Veg Sci* 5:213–226
- Zalba SM, Villamil CB (2002) Woody plant invasions in relictual grasslands. *Biol Invasions* 4(1–2):55–72