

Herbivory and the success of *Ligustrum lucidum*: evidence from a comparison between native and novel ranges

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Abstract. Invasive plant species may benefit from a reduction in herbivory in their introduced range. The reduced herbivory may cause a reallocation of resources from defence to fitness. Here, we evaluated leaf herbivory of an invasive tree species (*Ligustrum lucidum* Aiton) in its native and novel ranges, and determined the potential changes in leaf traits that may be associated with the patterns of herbivory. We measured forest structure, damage by herbivores and leaf traits in novel and native ranges, and on the basis of the literature, we identified the common natural herbivores of *L. lucidum*. We also performed an experiment offering leaves from both ranges to a generalist herbivore (*Spodoptera frugiperda*). *L. lucidum* was more abundant and experienced significantly less foliar damage in the novel than in the native range, in spite of the occurrence of several natural herbivores. The reduced lignin content and lower lignin:N ratio in novel leaves, together with the higher herbivore preference for leaves of this origin in the laboratory experiment, indicated lower herbivore resistance in novel than in native populations. The reduced damage by herbivores is not the only factor explaining invasion success, but it may be an important cause that enhances the invasiveness of *L. lucidum*.

Additional keywords: biological invasion, invasive woody species, natural enemies release hypothesis, evolution of increased competitive ability hypothesis.

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Introduction

Better understanding of why some invasive plants are more successful in their novel than in their native range remains as a major research priority in ecology. Several studies have indicated that natural enemies (such as herbivores, pathogens or parasites) may condition the abundance of plant species in their native range, and that their absence or reduction in the novel range enhances plant species fitness and demographic performance (Hufbauer and Torchin 2007). As a result, this reduction in natural enemies may explain why plants become so invasive in their novel range (enemy-release hypothesis, ERH; Elton 1958; Keane and Crawley 2002). Invasive plants that experience this enemy release may reduce their allocation of resources to defence traits (e.g. leaf toughness, phytochemical compounds) and, consequently, redirect resources to growth, thus increasing their competitive ability (evolution of increased competitive ability hypothesis, EICAH; Blossey and Nötzold 1995; Maron

et al. 2004; Bossdorf *et al.* 2005; Doorduyn and Vrieling 2011). The EICAH is then an expansion of ERH, although it is not necessarily a consequence, because the surplus of resources could be invested in diverse functional traits other than growth (Callaway and Ridenour 2004).

The ERH and EICAH have been discussed broadly in invasion ecology (Callaway and Ridenour 2004; Colautti *et al.* 2004; Dawson *et al.* 2014); however, few studies have provided empirical data that specifically support the predictions of these leading hypotheses. There has been some interesting research comparing traits of introduced invasive and native non-invasive plant species, often using congeneric species (Wolfe 2002; Colautti *et al.* 2004; Jogesh *et al.* 2008) and also studies that compare invasive and non-invasive introduced species in their novel range (Mitchell and Power 2003; Cappuccino and Carpenter 2005; Carpenter and Cappuccino 2005; Liu and Stiling 2006). Importantly, only a few studies (e.g. DeWalt

et al. 2004; Maron *et al.* 2004; Zou *et al.* 2008; Williams *et al.* 2010) have investigated the effect of enemies on some invasive species in their native and novel ranges. The comparison between both ranges might provide interesting insights and may help to achieve a more comprehensive view of species invasiveness (Hierro *et al.* 2005).

Despite the vast diversity and complexity of herbivores, plants and ecosystems, most studies have suggested that key leaf characteristics (physical and chemical) such as low structural compounds (carbon, lignin, cellulose or silica), high specific leaf area (SLA) and high nutrient and water content can increase palatability (Leoni 1997; Massey *et al.* 2007; Pérez-Harguindeguy *et al.* 2003, 2013). Usually, invader and non-invader plant species differ in their position in the leaf economics spectrum (Peñuelas *et al.* 2010). Specifically, successful invasive species tend to have traits that enhance rapid growth owing to increased photosynthetic capacity (e.g. high SLA, short leaf lifespan, high nutrient content; Smith and Knapp 2001; Lake and Leishman 2004; Grotkopp and Rejmanek 2007; Leishman *et al.* 2007; Montti *et al.* 2014) and this would potentially increase their palatability (Kumschick *et al.* 2013). Therefore, exploring the variation in foliar traits between native and novel genotypes can help to explain the potential differences in the preference of herbivores.

The main objective of our study was to compare the damage on leaves of a successful exotic invader in its native and novel range and explore differences in leaf traits that explain the potential differences in herbivory. We used *Ligustrum lucidum* W.T. Aiton (Oleaceae) as our case species and studied damage by herbivores by sampling populations of individuals growing under natural conditions in its native (China) and novel (Argentina) ranges.

Ligustrum lucidum, as other species of this genus, has a considerable number of natural herbivores in its native range, especially arthropods (mainly Lepidoptera and Coleoptera) and fungi (Shaw 1999). This species was introduced into several countries as an ornamental plant (Gavier-Pizarro *et al.* 2012; Guilhermetti *et al.* 2013) and has become a successful global tree invader outside its native range (Dascanio *et al.* 1994; Panetta 2000; Starr *et al.* 2003; Maddox *et al.* 2010; Aslan *et al.* 2012). In Argentina, the earliest records of *Ligustrum* spp. were cited near the 1900 (Sarmiento 1875; National herbarium record: Cabrera 2022, 7034 at the Darwinion Institute). In the past few years, *L. lucidum* has abruptly expanded its distribution, invading diverse ecosystems such as grasslands, dry, riparian and mountain cloud forests (Dascanio *et al.* 1994; Grau and Aragón 2000; Hoyos *et al.* 2010; Gavier-Pizarro *et al.* 2012; Aguirre-Acosta *et al.* 2014).

According to ERH and EICAH, we hypothesised that the release from its natural enemies and the potential reallocation of resources previously spent on defence to other functions such as growth may help to explain the increased abundance of *L. lucidum* in its novel range. Considering these hypotheses, we expect the following pattern in the novel range: (1) absence of natural herbivores, (2) reduced leaf damage in field conditions, (3) decreased allocation to herbivore resistance in leaves (e.g. increased nutrient quality and decreased lignin content) and, as a consequence, (4) increased herbivore preference for leaves from the novel range in an acceptability experiment.

Materials and methods

Studied species

Chinese glossy privet (*Ligustrum lucidum*) is an evergreen tree native from China, with a dense canopy and a height of ~15 m. It has small and white flowers arranged in upright panicles. Its fruits are an oblong blue black drupe of ~0.6 cm. Its distribution in the native range includes all Chinese provinces south of the Yangtze River and in the north, Shanxi and Gansu provinces (Chang *et al.* 1996). It grows between 0 and 2900 m above sea level in different climates and soil types, in full sunlight, as well as in shaded understory (Chang *et al.* 1996). It has been extensively cultivated for several years in China (where it is known as Nu Zhen 女贞) for different purposes (e.g. traditional medicine, culturing wax insects to obtain white wax, furniture). Because it is tolerant to air pollution, wind and poor soils, it was regarded as a great landscaping plant and planted extensively in streets and gardens. In its native range, it is rare in natural habitat (native forest) (L. Montti and M. M. Ayup, pers. obs.), which has been degraded or replaced by crops (e.g. rice, sugarcane) and cities since ancient times (Zhong and Qi-Guo 1998). In subtropical mountain forests of Argentina (i.e. novel range), it is by far, the most successful tree invader in secondary forest (Grau and Aragón 2000; Aragón and Morales 2003). It can form monodominant closed-forest patches, with evergreen crowns that reach the top canopy. It colonises even non-disturbed forest by recruiting in tree-fall gaps (Aragón and Morales 2003; Lichstein *et al.* 2004). Plant and animal diversity in these *Ligustrum*-dominated stands is significantly lower than in native ones, and the processes and ecosystem functions are altered at different temporal and spatial scales (Easdale *et al.* 2007; Hoyos *et al.* 2010; Aragón *et al.* 2014; Ayup *et al.* 2014; Zamora Nasca *et al.* 2014).

Study site

We sampled a total of 10 *L. lucidum* populations, including four in China, its native range, and six in Argentina, its novel range (Fig. 1). In both areas, we considered populations occurring along subtropical forest in similar (but opposite) latitudes (between 32 and 22° in both hemispheres). Particularly, subtropical evergreen broad-leaved forests were surveyed in China. The climate corresponds to a humid subtropical climate with monsoon influence. Annual mean temperature varied between 15°C to 22°C from the north to south with an annual rainfall between 1000 and 2000 mm. Relative altitudinal differences and soils types (Ultisols, Mollisols) are included in the studied area (He *et al.* 1998; Legendre *et al.* 2009; Domrös and Peng 1988). The studied sites in Argentina were secondary subtropical mountain forests. Climate is subtropical monsoonal with a marked dry winter season. Annual mean temperature varied between 22°C and 18°C from north to south, with an average annual rainfall between 1100 and 1500 mm (Brown and Kappelle 2001). Soils are diverse but predominately Mollisols of loam and sandy loam, with high concentrations of nitrogen and phosphorus (Soil Survey Staff 1999). Even though climate conditions may be similar in both ranges, there could be unaccounted differences in soil or microclimate characteristics among the populations.

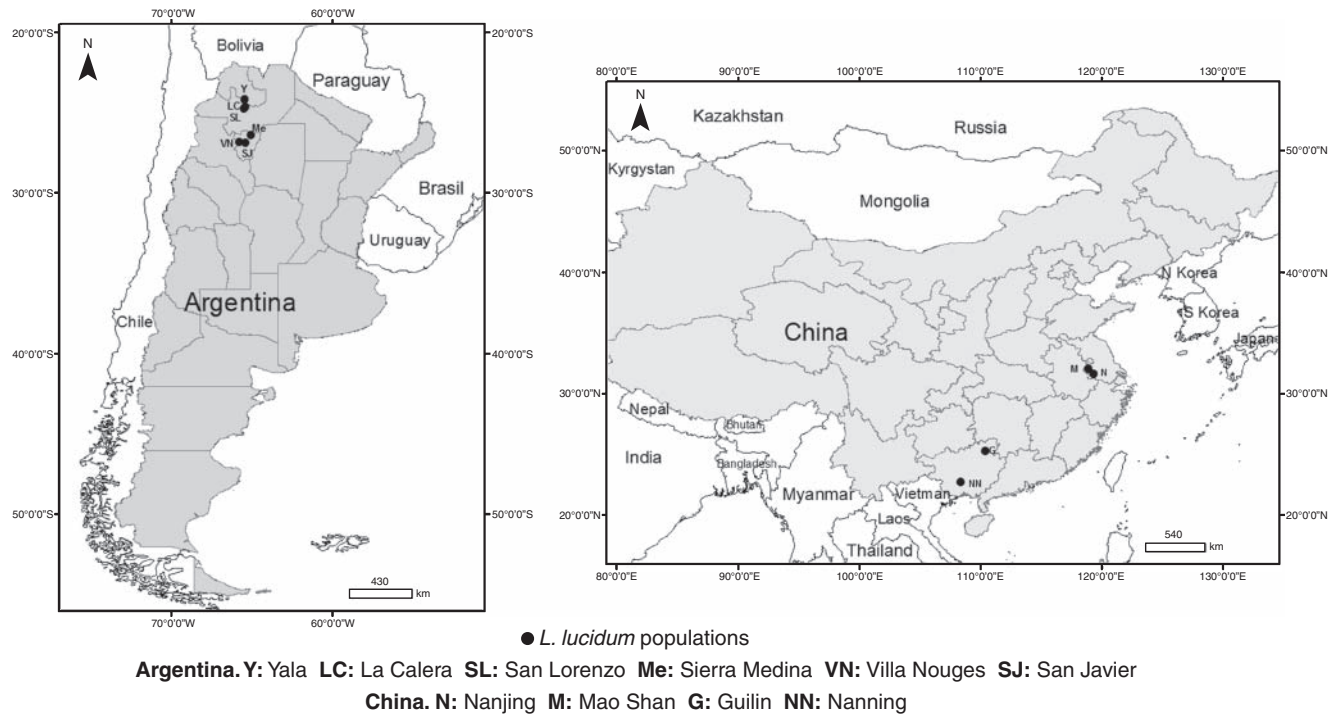


Fig. 1. *Ligustrum lucidum* populations in the study areas in north-western Argentina and south-eastern China.

Field work was conducted during spring–summer of 2013 in both countries (June to August in China and October to December in Argentina), coinciding with the period of greatest plant growth and herbivore activity. All populations in each country were more than 20 km apart from each other and represented discrete demographic units. However, because we did not perform genetic analysis, we cannot be sure that populations are genetically distinct.

Natural and new herbivore enemies

We refer to ‘natural’ enemies as those that are found in the native range (China), and potential ‘new’ enemies as those that are native to the invaded community (Argentina). We looked up at published information (e.g. Wu and Wu 1990; Cordo *et al.* 2004; Pastrana 2004; Zamudio and Claps 2005; Saini 2007; Konno *et al.* 2009; Li 2009; Xu 2009; Winks *et al.* 2012; Wang *et al.* 2013) and websites (e.g. <http://www.sinavimo.gov.ar>; <http://www.gbif.org>; <http://wbd.etibioinformatics.nl>, accessed 4 March 2014) to identify most important arthropod species (without differentiation between specialists or generalists) that were cited as feeding on *L. lucidum* leaf tissue or sap in China, and later, we checked whether these species were present in Argentina. In addition, we reviewed Argentinean literature records to identify any new potential *L. lucidum* generalist herbivores in its novel distribution.

Ligustrum lucidum forest description in native and novel range

To describe *L. lucidum* forest structure in its native and novel ranges, we established two plots of 25 × 25 m, separated by at least 50 m, in each of three randomly chosen populations per

range. Forest structure was evaluated by counting and measuring (height and diameter at breast height, DBH) all trees bigger than 10-cm DBH. The size of the plots was defined considering information from permanent plots established previously in a secondary forest of subtropical mountain forest of north-western Argentina (Grau *et al.* 1997). Our measurements included *L. lucidum* and all other species (natives and exotics).

Herbivory in native and novel ranges

We evaluated damage produced by herbivores in the field in six non-senescent, sun-exposed and fully expanded leaves of 10 individuals per population in both ranges during spring–summer. All individuals of *L. lucidum* were randomly selected and leaves of each individual were chosen randomly among three branches located in the same position of the tree. The proportion of leaf surface eaten was calculated using Image J version 1.42d (National Institute of Health, Bethesda, Md, USA). In addition, we used a 1 × 1 cm transparent grid paper to visually evaluate the fraction of total tissue that presented damage by herbivores and estimated a relative percentage of damage per pixel (1 cm²). We considered the following four types of damage: circular mines, serpentine mines, surface damage (chlorophyll stripped) and holes.

Herbivore acceptability

So as to quantify herbivore preference, we performed a laboratory experiment (Dirzo 1980; Pérez-Harguindeguy *et al.* 2003) in which we offered leaves from native and novel ranges to the generalist herbivore *Spodoptera frugiperda* (Lepidoptera, Noctuidae). Generalist herbivores such as *S. frugiperda* are frequently used to test species acceptability in laboratory

experiments (Dirzo 1980). We obtained the larvae from Estación Experimental Agroindustrial Obispo Colombres (EEAOC), Tucumán, Argentina. Three days before the beginning the experiment, we tested whether *L. lucidum* was toxic to *S. frugiperda*. For this, we used a subset of larvae and leaves from the novel range. Importantly, these larvae were reared on an artificial diet and, hence, were not exposed to *L. lucidum* (or any other plant tissue) before the experiment. In this way, we avoided any possible behavioural acclimation to *L. lucidum* in the novel environment. Twenty-four hours before the acceptability experiment started, *S. frugiperda* larvae were isolated and left without food to normalise appetite and facilitate feeding.

During the experiment, we allowed the larvae to feed on 2 × 2 cm samples cut from leaves of *L. lucidum* from the two origins, native (na) and novel (no). Fresh, fully expanded, non-senescent leaves from different trees, all randomly selected, were collected in China and Argentina simultaneously between 1 and 3 August 2013, 4 days before the experiment started. Leaves were kept in sealed plastic bags at 4–5°C and moisture was maintained with a humid paper cloth until processed. Subsequently, all samples were shipped to the Instituto de Ecología Regional (IER- UNT) in Argentina where the experiment was conducted.

The 2 × 2 cm leaf pieces were distributed in heterogeneous (na–no) or homogeneous (no–no or na–na leaves) pairs in separate Petri dishes. The paired squares were located at the opposite sides of each Petri dish and two larvae were placed in the middle. In the heterogeneous ones, we alternated the location of the pieces from the different ranges. The percentage of damage was estimated after 24 h. The percentage of herbivory was quantified visually by the same observer, using the following categories of percentage of tissue consumed: 0 = 0%, 1 = 0.1–6%, 2 = 6.1–12%, 3 = 12.1–25% 4 = 25.1–50% and 5 = 50.1–100%. The experiment included 53 and 25 heterogeneous and homogeneous pairs, respectively (i.e. 53 and 50 Petri dishes).

Using these herbivory categories, we calculated the herbivory index (HI) for each origin under field and experimental conditions as

$$HI = \sum ni \times i/N,$$

where ni = number of leaves per category, i = herbivory categories ($i = 0, 1, \dots, 5$) and N = total number of leaves per origin (Dirzo and Domínguez 1995).

Leaf-trait measurements

In both ranges, four or five individuals from each population were selected. The fully expanded, non-senescent and full-sun leaves were collected to measure several traits as indicators of leaf quality (nutritional and putative defence traits) potentially important to herbivores. The following traits were considered:

Leaf water content (LWC) was determined from five leaf samples per population that were stored in sealed plastic bags (moisture provided with a humid cloth) and kept at 4–5°C in the dark during transport to the laboratory. In most cases, samples were measured on the day of collection. Leaves were blotted dry with tissue paper to remove any

surface water, and immediately weighed. Leaves were then oven-dried in paper bags at 70°C until a constant weight, then reweighed to determine dry weight. LWC was computed as $LWC = (\text{fresh mass} - \text{dry mass})/\text{fresh mass}$.

Concentration of carbon and total leaf nitrogen were determined by dry-combustion method and using PerkinElmer 2400 Series II CHNS/O Elemental Analyzer (2400 Series II, Norwalk, CT, USA). Phosphorous concentration was determined using Easy Block Smart Digestor (Westco Scientific Instruments, Brookfield, CT, USA). All analyses were performed at the Universidad Nacional de Córdoba, Córdoba, Argentina. We used five samples per origin (native or novel).

Leaf tensile strength (LTS or leaf toughness) was measured as an index of leaf physical quality associated with physical protection (Vivanco and Austin 2006; Tecco *et al.* 2010) in five leaves from each origin (native or novel). A dynamometer constructed following Hendry and Grime (1993) was used and toughness was expressed as force per unit of width needed to tear apart a fresh leaf sample ($N\text{ mm}^{-1}$).

Specific leaf area (SLA) was measured as leaf area per dry weight ($\text{cm}^2\text{ g}^{-1}$). For this, fresh-leaf area was determined using ImageJ version 1.42d (National Institute of Health, Bethesda, Md, USA). Leaves were then oven-dried at 60°C until a constant weight, and SLA was computed as the ratio of the leaf surface to its dried weight ($\text{cm}^2\text{ g}^{-1}$). We used five to seven leaves per population.

Lignin, cellulose and hemicellulose were measured in five samples (of 4 g) from each origin. Percentages were determined by detergent method of Göering and Van Soest (1970) in Laboratorio de Nutrición y Forrajes INTA E.E.A. Bariloche, Río Negro, Argentina.

Data analysis

Student's *t*-tests were used to evaluate differences in forest structure, *L. lucidum* abundance and leaf traits between native and novel forests. Data were transformed to satisfy normality and homogeneity of variance assumptions. Field herbivory was analysed using ANOVA with a maximum-likelihood estimation and using a mixed model, with population and individuals (nested within population) as random effects, and accounting for heterogeneity of variances. The diversity in native and invaded forests was evaluated by Simpson's index. This index indicates the probability that two individuals randomly drawn from a sample are of the same species and it takes into account the number of present species, as well as the relative abundance of each species. Simpson's index is fairly independent of sample size, with values that range between 0 (infinite diversity) and 1 (no diversity) (Levenson and Stearns 1980). We used 1/D for Simpson's diversity measure because it corresponds with the 'effective number of species' and goes up as diversity increases. We used two response variables to evaluate herbivore preference (i.e. herbivore acceptability experiment), namely a binary variable (leaf square damaged or not damaged) and percentage of surface eaten. In the first case, we used a chi-square to test for differences in the distribution of leaf damage among the different origins, and in the second case, we used non-parametric Wilcoxon paired and Mann–Whitney tests

for heterogeneous or homogeneous arrays, respectively. All analyses were performed with InfoStat 2009 (Di Rienzo *et al.* 2009), its interface with R (R Development Core Team 2010) and R package nlme (for maximum-likelihood estimation with mixed models).

Results

Natural and new herbivore enemies

More than 25 arthropod natural-enemy species that affect leaves have been cited in *L. lucidum* native range (Appendix 1). Importantly, in its novel range, natural enemies such as *Chrysomphalus aonidium*, *Aonidiella aurantii* and *Pseudaulacaspis pentagona* were also recorded. These species are among the most important pests of cultivated trees in Argentina (e.g. lemon, orange and peach trees; Saini 2007; Zamudio and Claps 2005). In addition, more than 10 new herbivores that potentially produce damage to *Ligustrum* leaves in its novel range have been recorded by different authors (Cordo *et al.* 2004; Pastrana 2004).

Ligustrum lucidum forest description in native and novel range

In its native range, *L. lucidum* grows in subtropical evergreen broad-leaved forest where the dominant species are *Liquidambar formosana* (Altingiaceae), *Cinnamomum camphora* and *Cryptocarya concinna* (Lauraceae), *Osmanthus fragrans* (Oleaceae), *Aporosa yunnanensis* (Euphorbiaceae), *Cunninghamia lanceolata* (Taxodiaceae), *Castanopsis* spp., *Quercus acutissima*, *Q. glauca* and *Q. variabilis* (Fagaceae). In these forests, *L. lucidum* represented only 4% of the total basal area, occurred at densities lower than 35 individuals per hectare and the DBH class of 10–20 cm was prevalent. In contrast, in its novel range in Argentina, *L. lucidum* colonises secondary forest patches in the piedmont of subtropical mountain forests, where it forms almost monodominant thickets with a density of ~580 individuals per hectare. In these invaded patches, *L. lucidum* represents more than 60% of the total basal area in stands with extremely low diversity (Table 1). The dominant DBH class included individuals from 10 to 30 cm, being slightly bigger than in China. Native species such as *Cedrela lilloi* (Meliaceae), *Blepharocalyx salicifolius* (Mirtaceae), *Ocotea porphyrium* (Lauraceae), *Juglans australis* (Juglandaceae), *Allophylus edulis* (Sapindaceae), *Tipuana tipu* and *Parapiptadenia excelsa* (Fabaceae) were represented by few individuals.

Field herbivory in native and novel ranges

Damage by herbivores in the field was significantly lower in the leaves of trees colonising areas in the novel range, than in those

Table 1. *Ligustrum lucidum* forest structure and plant diversity (mean \pm s.e.) in native and novel ranges

LBA, *Ligustrum* basal area; TBA, total basal area. Simpson index⁻¹ increases in numerical value as species become more equitably distributed. * $P=0.07$, and ** $P<0.05$

Parameter	Native	Novel
Abundance (ind. ha ⁻¹)	32 \pm 13**	581 \pm 271
LBA/TBA (%)	4 \pm 1.2**	69 \pm 15
Simpson index ⁻¹	4.76 \pm 0.04*	1.85 \pm 0.18

growing in the native range (Fig. 2a). Variability among populations was higher in China, although, importantly, *L. lucidum* leaves there suffered more than twice the damage of those in Argentina in almost all types of leaf damage considered, including surface eaten ($t=2.51$, $P<0.05$, Fig. 2a, b), circular mines ($t=-2.13$, $P=0.05$, Fig. 2a, c), pixels with holes ($t=4.80$, $P<0.01$, Fig. 2a, d) or surface damage ($t=3.63$, $P<0.01$, Fig. 2a, e). Only for pixels with serpentine mines, differences were not detected ($t=0.54$, $P=0.60$, Fig. 2a, f). The HI in the field was also significantly higher in Chinese than in Argentinean leaves ($t=2.52$, $P<0.05$, Fig. 3).

Herbivore acceptability

In contrast to field measurements, when leaves from both native and novel habitats were offered simultaneously to a generalist herbivore in the laboratory experiment (*S. frugiperda*), the HI was higher for Argentinean leaves (no) ($t=8.26$, $P<0.01$, Fig. 3). When offered together, Argentinean leaves were selected 60% more often than Chinese leaves ($\chi^2=32.9$, $P<0.01$). On average, surface damage on Chinese leaves (na) was lower than on Argentinean leaves when offered in pairs (na–no; 0.44% and 7% for native and novel origin, respectively, Wilcoxon pair test $Z=5.72$, $P<0.01$) or separately (na–na or no–no; Mann–Whitney $U=82.5$, $P<0.01$). Considering only the heterogeneous pairs, the larvae also preferred Argentinean to Chinese leaves, whereas 4% of the time, the herbivore chose leaves from both origins, and only in ~3% of the cases they did not feed (Fig. 4a). Specifically, nearly of 60% of the Chinese leaves did not present any damage (Category 0) and only 20% presented moderate herbivory. On the contrary, leaves that came from the novel area showed, in most cases, moderate to high level of herbivory (Categories 1–3; Fig. 4b). There was no consumption under the highest-damage categories (Categories 4, 5) in leaves of any origin.

Leaf-trait measurements

Among leaves traits, SLA, LWC and LTS did not differ between leaves from the native and novel ranges (Table 2). Importantly, traits associated with herbivory resistance, such as lignin and lignin : nitrogen ratio, were highest in leaves from the native range. Chinese and Argentinean leaves also differed in nutrient concentration, with Chinese leaves having higher nitrogen percentage, and a tendency to have a lower carbon : nitrogen ratio.

Discussion

In the present study, we compared abundances, leaf damage by herbivores and several leaf traits on an invasive species in native and novel ranges. Our results indicated that the invasive tree *L. lucidum* is considerably more abundant and has significantly less damage by herbivores under field conditions in the novel than in the native range, in spite of the richness of natural enemies that was recorded in the novel range. The scarce leaf damage that plants in the novel range experienced may have caused the reduction in traits associated with herbivore resistance (i.e. reduced lignin, lower lignin : nitrogen ratio). This finding may explain the apparently contradictory results of the acceptability experiment, in which leaves from the novel range (that had reduced damage in the field), were significantly more frequently selected by the generalist herbivore *S. frugiperda*.

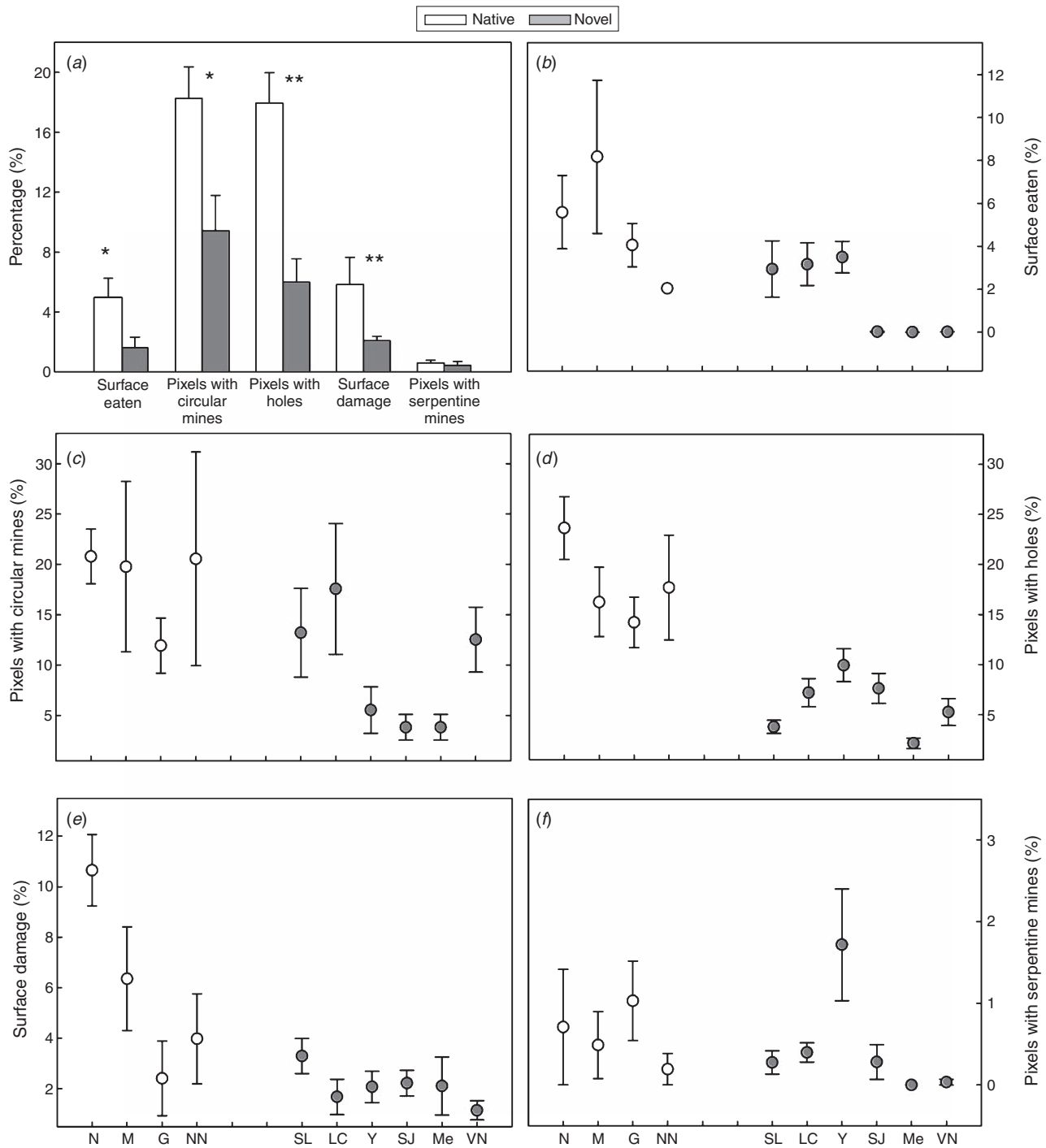


Fig. 2. Mean (\pm s.e.) percentage of leaf area under various types of herbivory (a) in the field in the native and novel ranges and (b–f) values per populations: N = Nanjing, M = Mao Shan, G = Guilin, NN = Nanning (China), SL = San Lorenzo, LC = La Calera, Y = Yala, SJ = San Javier, Me = Sierra Medina, VN = Villa Nougues (Argentina). * $P < 0.05$ and ** $P < 0.01$.

In the native range, a wide variety of specialist and generalist invertebrates were listed as *L. lucidum* natural enemies, and even though the leaves had defences against herbivory (i.e. higher lignin and lignin : nitrogen ratio), they showed important damage (Fig. 2). In the novel range, according to ERH predictions (Keane and Crawley 2002), we recorded less damage by herbivores than

in the native range. However, in our study system, as in other cases (Winks et al. 2012), natural and also new enemies of *L. lucidum* were registered in the novel range (Appendix 1). Therefore, the lower leaf damage in this range might be related to the potential reduction of some particular abundant enemy that occurs in China (but not in Argentina), rather than by the absence of

natural enemies. However, it is important to highlight that, in the present study, the impact of herbivores recorded in the field does not seem to be enough to explain, by itself, the success of this invasive species (the percentage of leaf surface eaten was rather low even in the species native range, Figs 2, 3). In addition, we acknowledge that there are several kinds of damage by herbivores that were not included in our assessments (e.g. removal of entire leaves, stem borers, gall makers, sucking insects that attack the stem, and belowground herbivores or fungal pathogens and soil microbes), and that may have significant effects on *L. lucidum* fitness. A more complete evaluation of the damage by herbivores is needed to fully test the ERH hypothesis. Also, as Siemann *et al.* (1998) and Hawkins and Porter (2003) demonstrated herbivore abundance and richness could be affected by plant community composition, richness and structure (e.g. plant species richness in *Ligustrum* forests is significantly lower than that in native forests). Future studies that include an evaluation of the role of plant community composition on the herbivore–invasive species interaction are necessary.

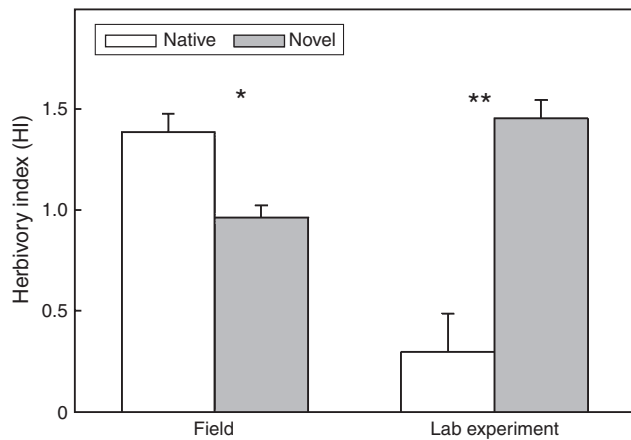


Fig. 3. Herbivory index (HI) in field and experimental conditions for *Ligustrum lucidum* leaves of native and novel ranges. * $P < 0.05$ and ** $P < 0.01$.

An alternative explanation for the reduced herbivory in the novel range may be related to the variability in leaf nutrient quality relative to the palatability of leaves from the co-existing plant species. Compared with other native plant species that co-occur in China, *L. lucidum* has a higher or similar nutrient quality (i.e. nitrogen percentage in the top quarter of 10 compared species; Liu *et al.* 2000; Wang *et al.* 2011). On the contrary, in Argentina, fresh leaves of *L. lucidum* recorded the lowest nitrogen concentration compared with the most common native tree species in the mountain forests (i.e. the nitrogen percentage in *Tipuana tipu*, *Ocotea porphyrium*, *Cupania vernalis* or *Cedrela lilloi* was double that of *L. lucidum*; Easdale 2006). This could potentially make *L. lucidum* less attractive to herbivores. Hence, the relative leaf quality may be more important than the lack of natural enemies in explaining the reduced damage on *L. lucidum* in natural conditions in the novel range.

The results of the acceptability experiment indicated that leaves from the novel range were preferred over the leaves from the native range when they were offered simultaneously to a generalist herbivore (*S. frugiperda*; Fig. 3). This preference contradicted the predictions based on their nutritional leaf quality (low nitrogen percentage, tendency of higher carbon : nitrogen ratio, both indications of low nutritional quality). Leaf physical resistance (i.e. lignin : nitrogen), which was lower in the novel leaves, may be more important in affecting the preference of *S. frugiperda*. As Aragón and Groom (2003) and Easdale (2006) showed, *L. lucidum* exhibits a higher growth rate, both as saplings and trees, than native species of subtropical mountain forests of north-western Argentina. This increased growth rate may be a consequence of the reallocation of resources caused by a reduction in damage by herbivores, following EICA hypothesis predictions, and as Siemann and Rogers (2003) and Zou *et al.* (2008) demonstrated for other invasive species. Nevertheless, resistance against specialist and generalist herbivores is generally based on different mechanisms and, importantly, invasive species differ in their responses to these two kinds of herbivores. Some invasive species reduce resistance to both generalist and specialist herbivores (Zou *et al.* 2008), whereas others increase resistance to generalists but reduce resistance

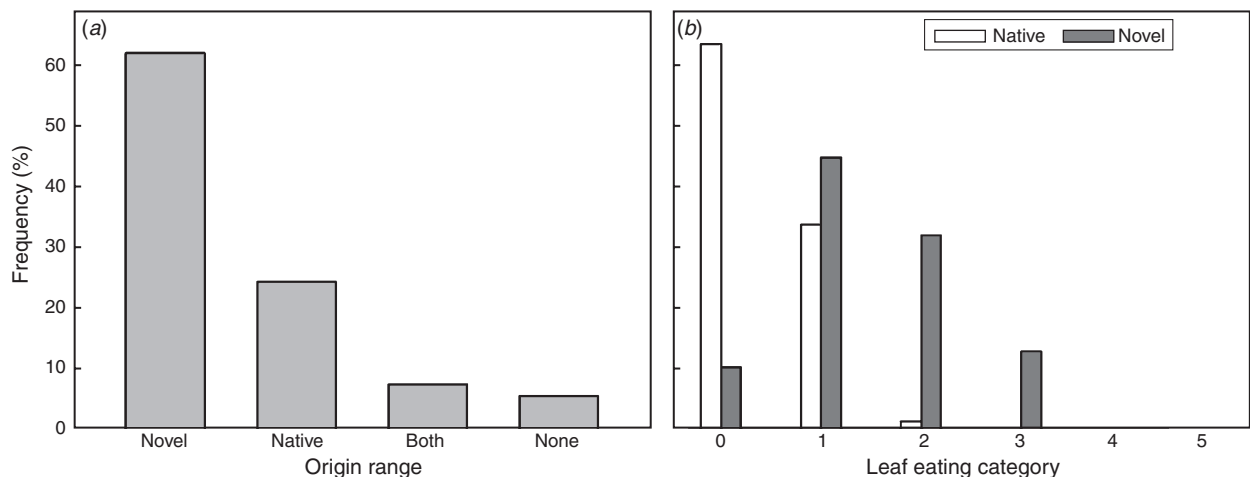


Fig. 4. (a) Frequency of leaves of the different origins eaten in the acceptability experiment. (b) Frequency of leaf damage per category. The categories correspond to leaf area consumed: 0 = 0%, 1 = 0.1–6%, 2 = 6.1–12%, 3 = 12.1–25%, 4 = 25.1–50% and 5 = >50%.

Table 2. *Ligustrum lucidum* leaf quality (mean \pm s.e.) in native and novel rangesLWC, leaf water content; SLA, specific leaf area; * $P=0.07$, ** $P < 0.05$, and *** $P < 0.01$

Parameter	Native	Novel
LWC (%)	67 \pm 0.98	68 \pm 4.68
Tensile strength (N mm ⁻¹)	0.71 \pm 0.02	0.75 \pm 0.02
SLA (cm ² g ⁻¹)	175 \pm 25	153 \pm 15
Lignin (%)	25.8 \pm 0.5	13.5 \pm 1.2***
Cellulose (%)	13 \pm 0.9	11 \pm 0.8
Hemicellulose (%)	9.2 \pm 0.6	14 \pm 0.6***
Carbon (%)	45 \pm 1.1	44 \pm 0.7
Nitrogen (%)	2.4 \pm 0.1	1.8 \pm 0.2*
Phosphorus (%)	0.25 \pm 0.01	0.22 \pm 0.04
Carbon : nitrogen	19 \pm 1.2	25 \pm 3.3
Lignin : nitrogen	11 \pm 0.8	7.5 \pm 0.8**

to specialists (Joshi and Vrieling 2005; Leger and Forister 2005; Müller and Martens 2005). Hence, our experimental results may have been different if we had used a specialist herbivore. In addition, there could be an alternative explanation to the experimental results that does not necessarily involve EICA hypothesis. Novel populations of *L. lucidum* may have derived from few individuals of certain Chinese populations that had poorer defences (low concentration of phytochemicals or poor structural defence), and, hence, individuals with these characteristics may have established in the novel range. As a consequence, leaves from the novel range would have become more palatable to *S. frugiperda*. This is known as ‘founder effect’ (Barton 1989) and describes the loss of genetic variation that may occur when a new population is established from a small number of individuals of a native population. Because *L. lucidum* has experienced horticultural selection pressure in China, and, consequently, its ‘native’ genetic variability may have been altered, this may have affected the variability of the invasive genotypes that arrived to Argentina in the past, and, therefore, potentially enhanced the importance of the founder characteristics. It is worth mentioning that these results could be species-specific (i.e. we used only *S. frugiperda* in our experiment). Thus, to discard this potential effect, new experiments including at least two more generalist species should be performed.

In summary, plant–herbivore interactions appear to be a complex process that add ambiguity to the field of invasion ecology. There are several reasons to doubt the ERH or EICA hypotheses as exclusive causes for invasive-species success (Callaway and Ridenour 2004; Colautti et al. 2004; Dawson et al. 2014), and our results do not clearly favour one over the other in the case of the invasive tree *L. lucidum*. The success of *L. lucidum* in the novel area can be explained by various factors such as propagule pressure, escape from root pathogens (Klironomos 2002; Callaway et al. 2011), environmental disturbances, and increased photosynthetic capacity or water use efficiency and higher reproductive success than the native species. Importantly, here we found that the decrease in herbivore damage might be another reason that potentially enhances the successful invasion by *L. lucidum*. This could depend not only on the absence (or reduction) of natural herbivores, but also on the relative difference in *L. lucidum* foliar traits (palatability)

when compared with the traits of the most common native species in the novel range. Common garden experiments using *L. lucidum* seeds from native and novel sources, growing with and without herbivores, would allow testing the effect of ‘origin’ in the competitive ability of this species, independently of environmental conditions (under the same climatic and soil conditions). It is also important to highlight that our findings are based on a fairly low sample size (i.e. 4 and 6 populations in China and Argentina respectively); therefore, increasing the number of replicates is strongly desirable. Genetic studies that explore the variability among populations in both ranges would also provide significant insights into the mechanisms governing the undesirable success of this invasive species. Last, our results showed that this invasive tree is indeed less affected by herbivores in the novel range, as ERH predicts. At the same time, some traits associated with herbivore resistance seem to be ameliorated in the novel range, and this would potentially free resources that could be redirected to growth, as EICAH predicts. This highlights the importance of comparative studies that include not only the introduced range, but also the native one. Logistic difficulties of this type of studies may limit the implementation of such comparisons (in our case these difficulties caused our restricted sample size). Developing strong international collaborations among scientific institutions in native and invaded ranges may facilitate this type of studies in the future.

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Appendix 1. Arthropod enemy species (leaf chewers or sap-sucking) of *Ligustrum lucidum* cited for native (China) and novel (Argentina) ranges
Pest, insect that also causes damage to agriculture by feeding on crops, or destroys garden plants

Order	Family	Species	Native	Novel	Pest
Acariformes	Eriophyidae	<i>Aceria ligustri</i> (Kiefer, 1938)	*		*
Acariformes	Eriophyidae	<i>Aculus ligustri</i> (Kiefer, 1938)	*		*
Coleoptera	Cerambycidae	<i>Batocera horsfieldi</i> (Hope, 1839)	*		*
Coleoptera	Cerambycidae	<i>Batocera lineolata</i> (Chevrolat, 1852)	*		*
Coleoptera	Cerambycidae	<i>Eutetrappa sedecimpunctata</i> (Motschulsky, 1860)	*		*
Coleoptera	Cerambycidae	<i>Trichoferus campestris</i> (Faldermann, 1835)	*		*
Coleoptera	Cetoniidae	<i>Clinteria ducalis</i> (White, 1856)	*		*
Coleoptera	Cetoniidae	<i>Euselates pulchella</i> (Gestro, 1891)	*		
Coleoptera	Cetoniidae	<i>Euselates quadrilineata</i> (Hope, 1831)	*		
Coleoptera	Cetoniidae	<i>Oxycetonia bealiae</i> (Gory et Percheron, 1833)	*		
Coleoptera	Chysomelidae	<i>Argopistes hoenei</i> (Maulik, 1934)	*		*
Coleoptera	Chysomelidae	<i>Argopistes tsekooni</i> (Chen, 1934)	*		*
Coleoptera	Chysomelidae	<i>Elythrosphaera vittata misionea</i> (Bechyné)		*	
Hemiptera	Aphididae	<i>Prociphilus ligustrifoliae</i> (Tseng & Tao, 1938)	*		*
Hemiptera	Cicadidae	<i>Cryptotympana atrata</i> (Fabricius, 1775)	*		*
Hemiptera	Coccidae	<i>Ceroplastes ceriferus</i> (Fabricius, 1788)	*		*
Hemiptera	Coccidae	<i>Ceroplastes japonicus</i> (Green, 1921)	*		*
Hemiptera	Coccidae	<i>Ericerus pela</i> (Chavanne, 1848)	*		*
Hemiptera	Diaspididae	<i>Acutaspis paulista</i> (Hempel, 1900)		*	*
Hemiptera	Diaspididae	<i>Acutaspis scutiformis</i> (Goethe, 1899)		*	*
Hemiptera	Diaspididae	<i>Aonidiella aurantii</i> (Maskell)	*	*	*
Hemiptera	Diaspididae	<i>Aspidiotus nerii</i> (Bouche, 1833)	*	*	*
Hemiptera	Diaspididae	<i>Chrysomphalus aonidium</i> (Linnaeus, 1758)	*	*	*
Hemiptera	Diaspididae	<i>Chrysomphalus dictyospermi</i> (Morgan, 1889)		*	*
Hemiptera	Diaspididae	<i>Mycetaspis personata</i> (Comstock, 1883)		*	*
Hemiptera	Diaspididae	<i>Parlatoria oleae</i> (Colvée, 1880)		*	*
Hemiptera	Diaspididae	<i>Pseudaulacaspis pentagona</i> (Targioni Tozzetti, 1886)	*	*	*
Hemiptera	Diaspididae	<i>Quadraspidiotus pemiciosus</i> (Comstock, 1881)	*		*
Hemiptera	Ericocidae	<i>Eriococcus lagerstroemiae</i> (Kuwana, 1907)	*		
Hemiptera	Fulgoridae	<i>Lycorma delicatula</i> (White, 1845)	*		
Hymenoptera	Formicidae	<i>Acromyrmex lundii</i> (Guérin-Méneville, 1838)		*	*
Lepidoptera	Arctiidae	<i>Halysidota ruscheweyhi</i> (Dyar, 1912)		*	
Lepidoptera	Geometridae	<i>Naxa seriaria</i> (Motschulsky, 1866)	*		
Lepidoptera	Crambidae	<i>Haritalodes derogata</i> (Fabricius, 1775)	*		*
Lepidoptera	Crambidae	<i>Palpita quadristigmalis</i> (Guenée, 1854)		*	
Lepidoptera	Crambidae	<i>Haritalodes derogata</i> (Fabricius, 1775)	*		*
Lepidoptera	Gelechiidae	<i>Parastega hemisigna</i> (Clarke, 1951)		*	
Lepidoptera	Pyralidae	<i>Locastra muscosalis</i> (Walker, 1866)	*		*
Lepidoptera	Saturniidae	<i>Automeris coresus</i> (Boisduval, 1859)		*	*
Lepidoptera	Saturniidae	<i>Automeris naranja</i> (Schaus, 1898)		*	
Lepidoptera	Saturniidae	<i>Hylesia nigricans</i> (Cramer, 1775)		*	*
Lepidoptera	Sphingidae	<i>Clanis bilineata</i> (Walker, 1866)	*		
Lepidoptera	Sphingidae	<i>Dolbina tancrei</i> (Staudinger, 1887)	*		
Lepidoptera	Sphingidae	<i>Kentrochrysalis streckeri</i> (Staudinger, 1880)	*		
Lepidoptera	Sphingidae	<i>Manduca rustica</i> (Fabricius, 1775)		*	*