



A Global Review of *Ligustrum Lucidum* (OLEACEAE) Invasion

Romina D. Fernandez^{1,6} · Sergio J. Ceballos¹ · Roxana Aragón^{1,2} · Agustina Malizia¹ · Lía Montti^{1,3} · Juan I. Whitworth-Hulse⁴ · Pilar Castro-Díez⁵ · H. Ricardo Grau^{1,2}

¹ Instituto de Ecología Regional (IER), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) - Universidad Nacional de Tucumán (UNT), Tucumán, Argentina

² Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán (UNT), Tucumán, Argentina

³ Instituto de Investigaciones Marinas y Costeras-CONICET, Instituto de Geología de Costas y del Cuaternario Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

⁴ Grupo de Estudios Ambientales – IMASL, Universidad Nacional de San Luis-CONICET, San Luis, Argentina

⁵ Departamento de Ciencias de la Vida, Facultad de Ciencias, Universidad de Alcalá, E-28805 Alcalá de Henares, Madrid, Spain

⁶ Author for Correspondence; e-mail: romi.d.fernandez@gmail.com

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Abstract

Ligustrum lucidum is a highly invasive East Asian tree that successfully colonizes several subtropical and temperate areas around the world. Its invasion capacity results from a widespread human use mostly in urban and periurban settings, very abundant fruit and seed production, small bird-dispersed fruits, high germination rates, resprouting capacity, fast growth rates, low herbivory levels and tolerance to a wide range of light, temperature and soil. All these traits contribute to its ability to rapidly increase in abundance, alter biodiversity, landscape ecology and limit its management. This paper reviews the current knowledge on *L. lucidum* with particular focus on its uses, distribution, invasiveness, ecological and economic impacts and control measures. Most relevant aspect of the review highlight the negative ecological impacts of *L. lucidum*, its potential to continue expanding its range of distribution and the need of further studies on the eco-physiology of the species, economic impact and social perception of its invasion and early warning systems.

Keywords Biological invasions · Ecological impacts · Glossy privet · Invasive tree species · Invasive plant control

Introduction

Invasive organisms are a distinctive feature of biological communities in the Anthropocene, particularly in peri-urban and human-disturbed ecosystems. Invasive

tree species are especially important because they may dominate primary production and vegetation structure, which in turn have large consequences for biodiversity and ecosystem services (Richardson and Rejmánek 2011). Many exotic tree species were introduced by humans to provide goods and services, such as shade and landscaping in gardens and urban settings, timber for construction, pulp for paper manufacture or edible fruits (Dickie et al. 2014; Castro Díez et al. 2019). However, once introduced, some of them can become invasive and displace native species, modify habitats, and affect ecosystem functioning and services (Vilà et al. 2011; Simberloff et al. 2013; Castro Díez et al. 2019).

Ligustrum lucidum (W. T. Aiton, Oleaceae) –glossy privet– is a tree species native to China. From there, it was transported to different countries worldwide since the eighteenth century as a garden and landscape ornamental tree and widely grown as hedging (Electronic Supplementary Material 1). Nowadays, it is considered as an invasive species in several countries (Richardson and Rejmánek 2011; Brixner Dreyer et al. 2019; CABI 2019).

Although *L. lucidum* invasion have been studied in great detail in some of the introduced areas (e.g., Argentina, Australia, Brazil and USA; eg. Mowatt 1981; Aragón and Morales 2003; Hoyos et al. 2010; Rodrigues et al. 2015; Van Oosterhout et al. 2016), knowledge gaps remain about how this species alter ecosystem functions and what happened in other areas where *L. lucidum* is also invasive. We believe that this review is necessary to summarize information about drivers, and consequences of the *L. lucidum* invasion and management and control tool used by this species as a prominent example of a globally successful invasive tree species.

Specifically, the aims of the present review are:

- Summarizing information on taxonomy, morphology and uses of the species.
- Providing an overview about *L. lucidum* distribution in its native area and in the invaded or novel ecosystems and potential distribution.
- Summarizing the life-history traits of *L. lucidum*.
- Describing its ecological and economical effects.
- Discussing hypotheses explaining the success of the *L. lucidum* invasion.
- Summarizing the prevention and control strategies used for this species.
- Identifying and highlighting the gaps in current knowledge to develop research priorities.

Methods

We reviewed numerous available sources of information in which *L. lucidum* appears as an invasive species including books, peer-reviewed articles, theses, technical reports and abstracts presented in scientific events using the following search engines: Google Scholar, Scielo and ResearchGate. We performed the search during November 2018–April 2019 using different combinations of the following keywords: “*Ligustrum lucidum*”, “glossy privet”, “broadleaf privet”, “large leaf privet”, “tree privet”, “ligustro”, “siempre verde”, “inva*” (i.e., invasive, invasion, invaded). In addition, we used other specific databases on invasive species or species distribution available on the Internet (Electronic Supplementary Material 2). This literature review was restricted

to studies published in English, Spanish and Portuguese and to studies that had information on uses of *L. lucidum*, its distribution; factors driving the successful invasion of the species, its impacts and control. We did not take into account studies focused on the anatomy, chemical composition or medicinal application of the species. We reviewed a total of 114 studies on *L. lucidum*. Most of the studies that specifically focused on *L. lucidum* invasion were carried out South American countries (Fig. 1). Therefore, this review may somewhat be biased towards describing the characteristics of the species' invasion in South American ecosystems.

The Species

A-Taxonomy and Morphology

Ligustrum lucidum belongs to the Oleaceae family, which contains a large number of invasive species (De Juana 2009). The species was described for the first time in 1810 by William Townsend Aiton in the Catalogue of the Plants Cultivated in the Royal Botanic Garden at Kew, London. Later, it was monographed by Decaisne (1879), Nakai (1921), Mansfeld (1924), Chang and Miao (1986), Yamazaki (1993), and De Juana (2009, 2014). Some authors describe this species as a shrub or small tree, while others considered it as a tall tree that can reach 20 m or more of height (Aragón and Morales 2003; Miller et al. 2013; De Juana 2014). This species has many similarities with other species of the genus *Ligustrum* (*L. japonicum* Thunb.) and it is sometimes misidentified (Johnson 2009; De Juana 2014), because of the uniform structure of the flower and the variability of characters such as indumentum and leaf shape and size (Kiew 1978).

The morphological characteristics of this species include the following: hairless leaves opposite each other, generally oval to elliptic in shape, 40–130 mm long, 30–60 mm wide, on petioles 10–20 mm long. Leaf tips taper gradually to a point while the bases are rounded. The upper leaf surface is dark green and glossy or shiny while the lower surface is paler with distinct venation. Flowers are fragrant, white or creamy,

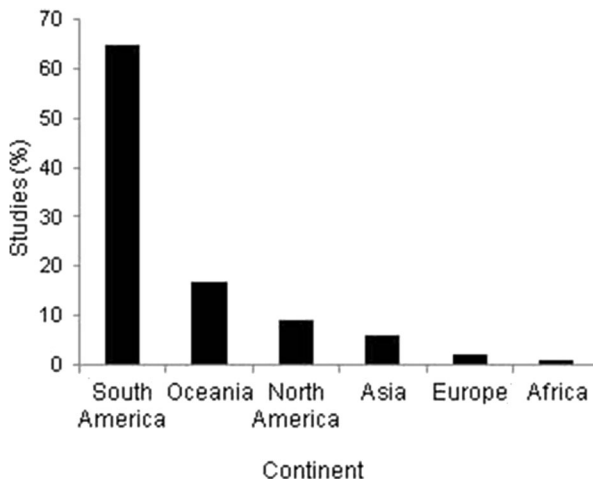


Fig. 1 Percentage of studies about *L. lucidum* invasion carried out in each continent

tubular in shape to 1.5 mm long, with lobes that are 2–4 mm long. The flowers are hermaphrodite and pollinated by insects (Johnson 2009; Aguirre-Acosta et al. 2014). The inflorescences are 100–250 mm long, 200 mm wide, and are broadly pyramid- to cone-shaped. *Fruits* are globular in shape, to 9 mm long and 12 mm in diameter, green when immature, turning blue to purplish-black in colour at maturity (Johnson 2009). *Seeds* are oval-shaped, 3–3.6 mm of diameter and 5–7 mm long, typically 1 or 2 per fruit, and their weight range is 18–73 mg (Montaldo 1993; Perez et al. 2001; Urcelay et al. 2019).

B-Uses

Ligustrum lucidum known as Nv Zhen (女贞) is a symbol of chastity in China (Stuart 1998) and has been extensively cultivated since ancient times for various cultural and medicinal purposes, such as culturing wax-insects to obtain white wax used for candles, as a polish for earthenware pots, book edges and for traditional medicine (Chang et al. 1996). In its native and introduced areas it is regarded as a great landscaping plant because it is tolerant to pest, air pollution, and wind; it grows fast even in poor soils, and provides a solid shade (Chang et al. 1996). The fruit is harvested when fully ripe and it is dried for later use (Bown 1995), i.e. it is often decocted with other herbs in the treatment of a wide variety of ailments and also as a general tonic (Duke and Ayensu 1985; Huang and Wang 2011; Zhang et al. 2011). However, there is some evidence that the fruits are toxic when eaten in high quantity (Bown 1995). Nowadays, the species main uses comprise small furniture manufacturers, agricultural tools, and as a supplement on food production or cosmetic products (e.g. soy sauce, toothpaste, etc.).

In the introduced area, *L. lucidum* was widely planted for hedge, shade, shelter and probably garden purposes because it is an attractive tree that gives good shade, grows rapidly and it produces fragrant flowers (Johnson 1953; Johnson 2009; Hoyos et al. 2010; Aguirre-Acosta et al. 2014; Hummel et al. 2014; Rodrigues et al. 2015). A study performed in New Zealand found that *L. lucidum* has a good wood for barbecue charcoal producing persistent heat (Wilcox 2000). Because of its hardness, *L. lucidum* wood has the potential to be used for rural constructions and posts (Schauman 2011; Benetti 2015). Due to its ability to grow in polluted environments, a study in Mediterranean cities suggested that *L. lucidum* can be useful to remove dust contaminants in urban environments (Oliva and Valdés 2004). Due to its phenology, shade and shape, forests invaded by *L. lucidum* are aesthetically appreciated and perceived as a cultural asset for ecotourism and outdoors recreational activities (Fernandez unpubl).

Distribution

L. lucidum in its Native Area

The native range of *L. lucidum* is generally considered to include all Chinese provinces south of the Yangtze River: Guandong, Guangxi, Guizhou, Hainán, Zhejiang, Fujian, Jiangxi, Yunnan, Gansu and Hunan (Chang et al. 1996; De Juana 2009); however, Wilcox (2000) consider that the native range is more extensive and include Anhui, Jiansu, and Tibet (Fig. 2a). In this wide native range it be found within the same type of

macroclimate, namely warm temperate (Brixner Dreyer et al. 2019), where the coldest month averaging between 0 °C-18 and at least one month averaging above 10 °C (Köppen-Geiger climate classification 1976–2000). According to biomes classification based on Olson et al. (2001), *L. lucidum* mainly occurs in the ‘Tropical and Subtropical Moist Broadleaf Forests’ (53%) and ‘Temperate Broadleaf and Mixed Forests’ (30%) (Fig. 2c).

The species can grow successfully between 0 to 2900 m.a.s.l and in different soil types, both in full sun and in deep shade, being able to resist frosts of −15 °C (Chittendon 1956; Davis 1990; Editorial Committee of the Flora of China 1992; Montti et al. 2016). Currently, the species is mostly found planted in urban areas along

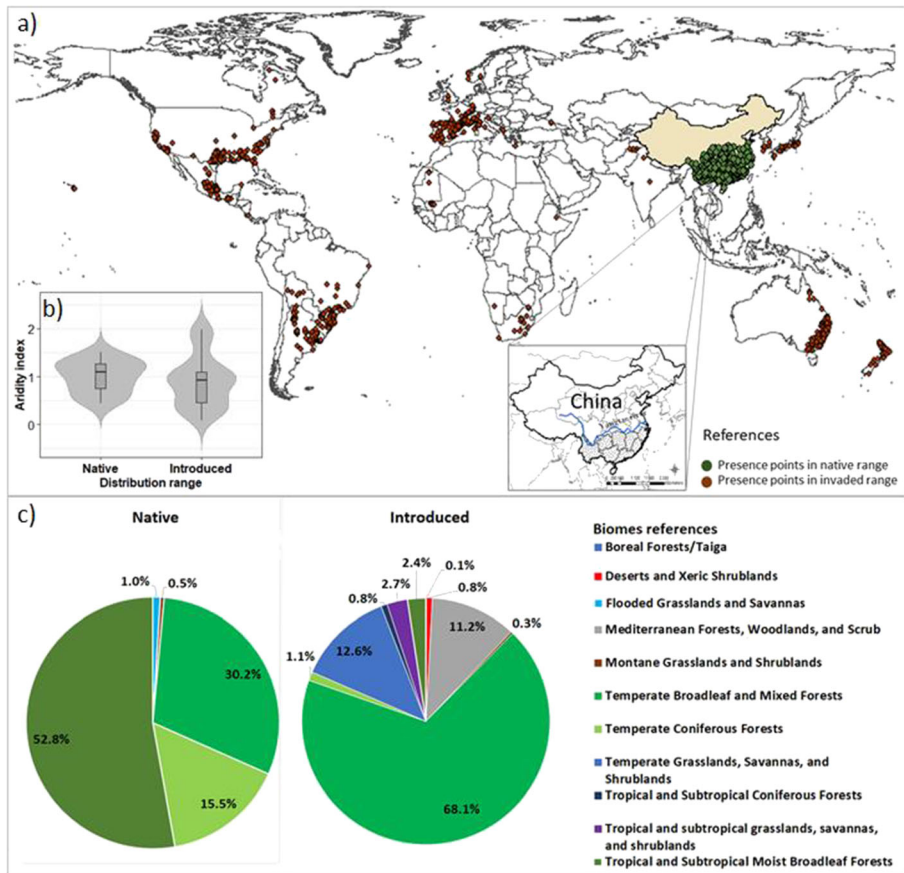


Fig. 2 a) Presence of *L. lucidum* in its native (green dots) and introduced (orange dots) distribution range. A zoom in China show the provinces where *L. lucidum* is currently distributed (Chang et al. 1996). b) Violin plots showing the aridity index in the native and introduced range of *Ligustrum lucidum*. The width of each violin plot refers to the density of occurrence data points and the boxes indicate the interquartile range. Climate classes based on global aridity index values (Trabucco and Zomer 2009) are “Hyper Arid” (< 0.03), “Arid” (0.03–0.2), “Semi-Arid” (0.2–0.5), “Dry sub-humid” (0.5–0.65), and “Humid” (> 0.65). c) Percentage of *L. lucidum* occurrence both in native and introduced biomes (Based on Olson et al. 2001). Georeferenced occurrence points (i.e., native and introduced distribution range) were obtained from CABI database (CABI 2019), GBIF database (GBIF, 2019) and personal observations

all China and it is very rare to find it in native forests (Montti et al. 2016), which has been for the most part transformed or replaced by crops (e.g., rice, sugar cane) and rapid urbanization (Zhong and Zhao 1998; Miao et al. 2013).

***L. lucidum* in the Invaded Range**

Currently, there are abundant records of *L. lucidum* in North America, South America, Europe, Asia, Africa and Oceania (Brixner Dreyer et al. 2019) and it seems to exist few environmental barriers to seed production and propagation of this species (Aslan et al. 2012). The invaded range of *L. lucidum* included areas with temperate climate similar to its native range, as well as warmer and wetter, semi-arid and arid areas revealing a climatic niche shift during global scale invasion (Hashimoto et al. 2007; Guidini et al. 2014; Montti et al. 2017, Brixner Dreyer et al. 2019; based on Köppen-Geiger climate classification 1976–2000; Fig. 2b). This wide climatic amplitude influences its abundance in the different regions (Fig. 2c; biomes based on Olson et al. 2001). *L. lucidum* occurrence in the introduced range is almost unrepresented in this ‘Tropical and Subtropical Moist Broadleaf Forests’ and the percent in the ‘Temperate Broadleaf and Mixed Forests’ biome climbs up to 68%. *L. lucidum* have been also introduced in new biomes worldwide (Carr et al. 1992; Swarbrick et al. 1999; Australia’s Virtual Herbarium, 2008; Montti et al. 2017), highlighting their occurrence in the ‘Temperate Grasslands, Savannas, and Shrublands’ and ‘Mediterranean Forests, Woodlands, and Scrub’ (Fig. 2c). Accordingly, the introduced range of *L. lucidum* – based on Brixner Dreyer et al. (2019) and own data of biomes (obtained from presence points from the GBIF database, CABI database and personal observations) –, suggest a severe threat for the ecosystems in temperate areas. *L. lucidum* shows resistance to low temperatures and ample humidity tolerance (Dascanio et al. 1994; Guilhermetti et al. 2013; Brixner Dreyer et al. 2019). Its rapid adaptation to the cities is possible partially because *L. lucidum* has tolerance to pollution (McGregor 2000; Oliva and Valdés 2004; García-Sánchez et al. 2019). This capacity is relevant because cities are often a source of propagules promoting the invasion of *L. lucidum* into neighboring natural landscapes (Montti et al. 2017). Under this situation and according to the current invasive distribution range, we are wondering if the temperate environments are more prone to invasion or these environments are more invaded as a consequence of the legacy of human dispersal into these sites. Thus, following humans and other animals ‘dispersion increase, it is expected that *L. lucidum* will continue expanding its distribution range towards diverse and contrasting biomes, becoming potentially a serious invasive species in many places.

Life-History Traits of *L. lucidum*

Ligustrum lucidum have several characteristics at different stages of the life cycle that enhance the invasion success. These characteristics reflect the investment of *L. lucidum* in germination, reproduction, seed dispersal growth and biotic interactions (Table 1).

Table 1 Characteristics of the life cycle of *Ligustrum lucidum*

| Life stage | Characteristic | References |
|------------|---|--|
| Seeds | Can germinate after bird dispersal but also from fallen fruits. High germination rate (70–95%). | Montaldo (1993); Panetta (2000); Aragón and Groom (2003); Powell and Araújo (2017) Fox and Adamson (1986); Ekert and Bucher (1999); Montaldo (2000); Aguirre-Acosta et al. (2014); Diaz Villa et al. (2016) |
| Seedlings | Capable of germinating in different environments (gaps, edges and under the forest canopy). Germination is possible under levels of 1–5% full sunlight. High density of seedlings in invaded areas (200 to >600 per m ² or 10–1000 in a radius of 4–5 m around adults). Higher survival than other tree species both in gaps and under the canopy. | Buchanan (1989); Aragón and Groom (2003) Adamson and Buchanan (1974); Fox and Adamson (1986); Buchanan (1989); Johnson (2009); Brazeiro (2018) Aragón and Groom (2003) |
| Saplings | Recruitment is favoured by some tree or shrub cover (nurse effect). | Malizia and Greslebin (2000); Aragón and Morales (2003); Tecco et al. (2006, 2007); Giantomasi et al. (2008) |
| Adults | Higher diameter growth rates than native tree species. Early sexual maturity (at a minimum dbh of 6.4 cm; < 10 years). Monoica Insect pollination High fruit production. A tree can produce in one year 15,316 fruits. Prolonged period of fruiting (8 months). Seed production in one year could be as high as 100,000–10,000,000 seeds per tree Maximum height 17–20 m Clonal reproduction Can live for 50–100 yr but sprouts make trees far long-lived. | Aragón and Groom (2003) Aguirre-Acosta et al. (2014) Johnson (2009) Johnson (2009); Aguirre-Acosta et al. (2014) Westoby et al. (1983); Ferreras et al. (2008) de Oliveira et al. (2016) Fox and Adamson (1986); Ekert and Bucher (1999) Aragón and Groom (2003); www.ambienteforestalnoa.org.ar Lichstein et al. (2004); Batista and Biondi (2009); Johnson (2009); Hoyos et al. (2010); Diaz Villa et al. (2016); Malizia et al. (2017); Franco et al. (2018) Swarbrick et al. (1999) |

Table 1 (continued)

| Life stage | Characteristic | References |
|------------|---|---|
| | Have straight trunks and branch high without intermingling their crowns. | Dascanio et al. (1994); Hoyos et al. (2010); Guilhermetti et al. (2013); Ayup et al. (2014) |
| | Faster diameter growth rates than other tree species (0.69 mm yr ⁻¹). | Malizia et al. (2017) |
| | Tolerance of the pollution of the cities | McGregor (2000); Oliva and Valdez (2004); Garcia-Sánchez et al., (2019) |
| | Recruitment in open sites and in closed-canopy forests (shade-tolerance). | Grau and Aragón (2000); Aragón and Morales (2003); Gurvich et al. (2005); Hoyos et al. (2010); Guilhermetti et al. (2013); de Souza Nogueira (2017); Franco et al. (2018); Whitworth Hulse (2018) |

Germination

L. lucidum has the ability to germinate in gaps, edges and under the forest canopy, both from fallen fruits and bird-dispersed seeds (Montaldo 1993; Panetta 2000; Aragón and Groom 2003). Although germination can be partially inhibited in fallen fruits (Burrows and Kohen 1986), *L. lucidum* fruit production is so abundant and that fallen fruits still can account for a significant part of the seedlings established (Table 1; Montaldo 1993; Aragón and Groom 2003). Bird-dispersed seeds have a high germination rate, which also represents an advantage for this species (Fox and Adamson 1986; Ekert and Bucher 1999; Montaldo 2000; Aguirre-Acosta et al. 2014; Diaz Villa et al. 2016).

Seed Banking and Seedling Establishment

Although *L. lucidum* does not form a long-term seed bank it is able to establish transient soil seed bank (Panetta 2000). The most propagules survive for less than 12 months (Panetta 2000). Also, under field conditions the seed survival is high over the initial 6 months mainly surface-sown (Panetta 2000). Germination results in a high density of seedlings which vary broadly in invaded areas (Table 1). The seedlings have higher survival than other tree species both in gaps and under the canopy (Aragón and Groom 2003).

Reproduction

At the reproductive stage, *L. lucidum* has the advantage of reaching sexual maturity early and the capacity to reproduce also clonally (Table 1). Clonal reproduction occurs from sprouts that emerge from the base of the stem and roots and represents an advantage for the persistence of the invasion through time (Grau and Aragón 2000; Batista and Biondi 2009; Johnson 2009). These basal resprouts can grow and dominate the canopy when the breakage of the main stem occurs (Aragón and Morales 2003; Johnson 2009). Sexual reproduction of *L. lucidum* results in a high production of fruits and seeds (Table 1), which represent an important propagules input that drives the invasion (Montaldo 1993; Montaldo 2000; Ferreras et al. 2008; Emer et al. 2012). Nevertheless, the fruit and seed production of *L. lucidum* can widely vary with tree size, across years and environmental conditions (Westoby et al. 1983; Aguirre-Acosta 2016).

Seed Dispersal

This species is dispersed by several fruit-eating birds that facilitate the population growth of *L. lucidum* through different egestion modes (i.e. defecation or regurgitation of seeds; Montaldo 2000; Aragón and Groom 2003; Powell and Aráoz 2017). A study in subtropical Argentina found that fleshy-fruits of *L. lucidum* show similar chemical and morphological traits than fleshy-fruits produced by native species, and thus its dispersal can benefit from existing animal mutualism interactions and integrate within the native community (Rojas et al. 2019). This species also, offers fleshy fruits to birds during periods when other food sources are limited (Carr et al. 1992; Montaldo 1993; Ekert and Bucher 1999; Grau and Aragón 2000; Ferreras et al.

2008). Additionally, *L. lucidum* can have an extended period of fruiting (Table 1), which may also contribute to its invasion success (de Oliveira et al. 2016).

Recruitment

Ligustrum lucidum can recruit and survive in a wide range of environments (Aragón and Groom 2003; Ito and Fujiwara 2007; Tolocka 2017), but particularly under shade conditions (Buchanan 1989; Hoyos et al. 2010; Demers et al. 2012; Zamora Rivera 2016; de Souza Nogueira 2017; Franco et al. 2018; Whitworth Hulse 2018). *L. lucidum* behaves as a shade-tolerant or late-succession species (strategy k) by recruiting under shrubs and trees that provide a less harsh environment, protection from trampling and browsing, and perches for bird dispersers (Grau et al. 1997; Malizia and Greslebin 2000; Tecco et al. 2006; Tecco et al. 2007; Giantomasi et al. 2008; Powell and Aráoz 2017). This shade tolerance gives the advantage of invade undisturbed forest patches and persist throughout the time in invaded forests (Goya et al. 1992; Aragón and Morales 2003; Gurvich et al. 2005; Gavier-Pizarro et al. 2012; Hoyos et al. 2010; Malizia et al. 2017; Franco et al. 2018).

Growth Rate and Competitive Ability

Ligustrum lucidum has been reported to grow fast and can live about 100 years (Table 1) allowing to reach the canopy and create conditions that influence negatively on native communities (Aragón and Groom 2003; Easdale et al. 2007; Batista and Biondi 2009; Hoyos et al. 2010; Ayup et al. 2014). Invaded forests are dense because *L. lucidum* have straight trunks and branch high without intermingling their crowns, and has less cover in the herbaceous and shrubby strata (Dascanio et al. 1994; Hoyos et al. 2010; Guilhermetti et al. 2013; Ayup et al. 2014; Van Oosterhout et al. 2016). This structure creates low light conditions in the understory, hampering the establishment and growth of most species of trees, shrubs and climbing plants, ultimately resulting in the dominance of *L. lucidum* and the exclusion of native species (Grau and Aragón 2000; Lichstein et al. 2004; Hoyos et al. 2010; Ceballos et al. 2015; Ferrero et al. 2017; Ferreras et al. 2019). Only large trees survive within invaded forests, for example *Lithraea molleoides* in dry forests of Argentina, *Ocotea porphyria* in subtropical montane forests of NW Argentina, and *Eucalyptus* spp. in Australia (Swarbrick et al. 1999; Hoyos et al. 2010; Zamora Rivera 2016; Franco et al. 2018). Also, *L. lucidum* has the ability to establish symbiotic mutualistic associations with mycorrhizal fungi with the phylum Glomeromycota as was registered in dry forests of Central Argentina (Herrera et al. 2016) that might foster upper its range expansion over non-invaded higher elevations (Urcelay et al. 2019).

Ecological Effects of *L. lucidum* Invasion

Impacts of *L. lucidum* over Native Biodiversity

In general, monodominant *L. lucidum* forests has lower species richness, diversity and equitativity than native forests of similar ecosystems. This pattern was found when considering trees in subtropical montane forests of NW Argentina (Lichstein et al.

2004; Grau et al. 2007, 2008; Zamora Rivera 2016; Flombaum et al. 2017), dry forests and shrublands of Central Argentina (Hoyos 2007, 2010; Furey 2010; Giorgis and Tecco 2014; Giorgis et al. 2017), coastal of Central Argentina (Diaz Villa et al. 2016) and temperate forests of USA (Garza and Bratton 2008). Consistently, the soil seed banks of woodlands dominated by *L. lucidum* have a lower total seed density and richness compared to native woodlands (Ferrerias et al. 2015). However, this pattern is less clear for other groups of organisms or even for understory plants or tree saplings. Contrastingly, the richness of native trees, tree saplings and shrubs in the sub-canopy or understory strata was not correlated with *L. lucidum* dominance in a subtropical montane forest of NW Argentina (Lichstein et al. 2004; Bartolucci 2011). An increase in native tree species mortality (Franco et al. 2018) or a reduction in growth rate (Malizia et al. 2017) may affect native species at different life stages (i.e., germination, seedling survival or saplings growth) and hence reduce native tree species richness.

L. lucidum invaded forest has approximately half the species richness of climbing plants when compared with native dry forest of central Argentina (5.25 and 11 for *Ligustrum* and native forest, respectively; Ferrero et al. 2017), and in a subtropical montane forest of NW Argentina (6 and 10 species for *L. lucidum* and native forest, respectively; Ceballos et al. 2015). Reduced tree species richness, low light availability (Lichstein et al. 2004; Ayup et al. 2014, Ayup 2016; Ferreras et al. 2019), and characteristic of *L. lucidum*'s bark are cited as potential causes of the reduction in species and functional diversity of woody climbers (Ceballos et al. 2015). Species richness of other groups of organisms, such as soil fauna (Fernandez 2018) and microflora (Fernandez et al. 2017) may be also affected in different ways by changes that *L. lucidum* invasion generates in litter quality, soil chemistry and micro-environmental conditions. Order richness of soil fauna was similar in *L. lucidum* and native riparian and Serrano forest of Uruguay (Brazeiro 2018), and the same was true for beetle species richness in *L. lucidum* and native forest of Auckland city in New Zealand (Blanchon et al. 2011). A contradictory pattern was found for spider species or morphospecies richness in Espinal forest of Entre Rios, Argentina. *L. lucidum* forest had not only lower spider species richness, but also lower functional richness (Almada and Sarquis 2016). Evenness may change without a significant alteration of species richness, as in the case of edaphic fauna in forest of Uruguay that was reduced in *Ligustrum* forest where the order Astigmata represented more than 90% of the collected individuals (Vettorazzi et al. 2018).

L. lucidum invasions might be expected to enhance populations of frugivorous birds because, in many parts of its new range, *L. lucidum* fruiting season coincides with the season of low fruit availability (e.g. Brazil, de Souza Nogueira 2017; and Argentina, Ferreras et al. 2008). However, Ayup et al. (2014) found that bird species richness, diversity and abundance were lower in *L. lucidum* invaded forest than in native secondary forest of similar successional age in NW Argentina, and this was true even during the dry season (i.e., *L. lucidum* fruiting season). This suggests that *L. lucidum* mostly favours generalist frugivorous birds, such as the ubiquitous *Turdus rufiventris* and *Thraupis sayaca*, both found to be dominant in *L. lucidum* forest (Ayup et al. 2014). In coastal forest of temperate Argentina, Montaldo (1993) found that the frequency of some bird species was higher during the fructification in *L. lucidum* forest, but they provide no data about the comparison of total species richness in both forest types in this ecosystem.

Biomass Accumulation and Carbon Sequestration

In its native range, Montti et al. (2016) observed that *L. lucidum* presented densities lower than 35 individuals per hectare, most of them belonging to the 10–20 cm dbh class. In contrast, in its novel range in subtropical montane forests of NW Argentina, *L. lucidum* may form a monodominant secondary forest that stands out for its high values of aboveground biomass. A study in this region compared two chronosequence monitored through time where successional forests have the same age (mean stand age = 30 yr), registered that secondary forests dominated by *L. lucidum* showed approximately twofold values of tree biomass than secondary forests dominated by native species (345–394 Mg ha⁻¹ in *L. lucidum*-invaded forests vs 135–264 Mg ha⁻¹ in native forests (Malizia et al., unpublished data). Moreover, *L. lucidum*-invaded forests showed an increment in biomass of 9.6 Mg ha⁻¹yr⁻¹ while native secondary forests increased 5.16 Mg ha⁻¹yr⁻¹, likely due to *L. lucidum* highest growth and recruitment rates, and the lowest mortality compared to native tree species (Easdale et al. 2007; Malizia et al. 2017). Studies on belowground biomass are much more limited, but the biomass of fine roots (i.e. < 1 mm) was higher in *L. lucidum* invaded patches of dry forests of Central Argentina compared to native-dominated patches in the same region, and in humid forest of Australia was observed dense mats of fibrous roots near the ground surface (Johnson 2009). This pattern may influence ecosystem functioning by increasing the efficiency of water and nutrient consumption of the surface soil (Johnson 2009).

Water Dynamics

Studies assessing the variation among the year of the normalized difference vegetation index (NDVI), used as a proxy of transpiration (Zhang et al. 2001), show higher values in *L. lucidum* – invaded forests than in native forests, particularly during the dry season, in subtropical montane forests of NW Argentina and dry forests of Central and northern Argentina (Hoyos 2007; Zamora Nazca et al. 2014; Whitworth Hulse 2018). Zamora Nazca et al. (2014) and Whitworth Hulse (2018) found that *L. lucidum*-invaded forests present 15% less annual average water content than adjacent native forests, and these differences increased to values of 30%, during the dry season. Deep soil water availability of small catchments is also lower in *L. lucidum*-invaded forest than in native forests dominated by *Lithraea molleoides* in dry forests of Central Argentina (Whitworth Hulse 2018), suggesting a reduction of groundwater recharge. Consequently, streamflow could be also altered, reducing downstream water provision services during dry season, not only in water-limited ecosystems in Argentina, but also in other drylands worldwide where *L. lucidum* is invading, such as riparian areas of United States (Sung et al. 2011), Australia (Lymburner et al. 2006) and South Africa (Meek et al. 2010).

Litter Decomposition and Nutrient Cycling

In riparian forests of central Argentina, *Ligustrum lucidum* produces more litter than most native species and its litter has lower lignin and phenols than the dominant native species *Pouteria salicifolia*, which explains the higher decomposition rate of *L. lucidum* (Dascanio et al. 1994; Marano et al. 2013). In contrast, in a subtropical montane forest of NW Argentina Ayup et al. (2014) found less litter in the forests invaded by

L. lucidum than in native forests; however *L. lucidum* litter showed lower cellulose and lignin content than that of two abundant native tree species *O. porphyria* and *C. vernalis* (unpublished data), which may explain the higher litter decomposition rate of *L. lucidum* in this area (Aragón et al. 2014a; Fernandez and Aragón 2014). Contrary to these findings, the decomposition rate of *L. lucidum* is slower than that of native species in forests of Uruguay (Fariás et al. 2018).

The variability in litter quality between *L. lucidum* and native species of the different invaded ecosystems is reflected in decomposition rate at ecosystem level. Fernandez (2018) found that decomposability (in a “common garden” with standard conditions) and in situ decomposition of litter mixtures from forests invaded by *L. lucidum* were greater than that of the native forest in a subtropical montane forest of NW Argentina. Thus, *L. lucidum* could accelerate the rate of litter decomposition in this ecosystem and speed up the nutrients cycling. Consistently, Aragón et al. (2014b) found that sites invaded by *L. lucidum* had lower N concentrations and higher activity of soil enzymes related to litter decomposition (20 and 30% increases in β -glucosidase and alkaline phosphatase activity) than the native forest, suggesting that *L. lucidum* invasion accelerates nutrient uptake and nutrient-cycling rates, particularly N cycling (Aragón et al. 2014b). However, Furey et al. (2014) observed that in dry forests of Central Argentina, the decomposability of litter mixtures from *L. lucidum* forests was lower than that of native forests, which could slow the rate of decomposition of this ecosystem. This result highlights the context-dependency of *L. lucidum* invasion on litter decomposition rates, as previously highlighted for other invasive species (e.g. Castro-Díez et al. 2014).

Economic Effect of *L. lucidum*

The economic impact of *L. lucidum* invasion has been much less studied than its ecological impacts. To date, there are no studies on the costs of *L. lucidum* invasion and very few studies reported the control costs (see Johnson 2009; Haretche and Brazeiro 2018; Valfré-Giorello et al. 2019). Through disrupting ecosystems, *L. lucidum* could influence (negatively or positively) human quality of life by affecting security, food and health. For example, in Australia and New Zealand, mature trees of *L. lucidum* on abandoned land and ruderal habitats have been reported to interfere with power and telephone lines (McGregor 2000); besides, the flowers of *L. lucidum* compete for bees, which may reduce the pollination of desirable crops like kiwifruit (Syrett 1987). In USA, Spain, Australia and New Zealand *L. lucidum* pollen has been reported to cause hay fever, asthma and other respiratory allergies (Wodehouse 1971; McGregor 2000; Cariñanos et al. 2002; Van Oosterhout et al. 2016) though there is no clinical evidence of this effect. It is possible that this invasive species has a positive economic impact through the use of its wood and ecotourism (see section Uses). Also, high carbon sequestration rates may translate into economic benefits in schemes of carbon markets.

Hypothesis to Explain Invasion Success

Global dissemination of *L. lucidum* appears to be related to several factors: First, China –its native country– is the most populated country in the world, a major center of

species domestication (including for example some of the most successful crops such as rice, soybean, sugar cane and citrus), and has an increasingly intensive trade with all continents, which may have facilitated cultural influence and spread around the world. Second, the adoption by local urban and periurban environments promote the widespread distribution of the introduction points (Grau and Aragón, 2000; Montti et al. 2017). Third, *L. lucidum* has an efficient dispersal from the centers of introduction and shows a wide climatic amplitude (Montti et al. 2017; Brixner Dreyer et al. 2019).

Different studies provided empirical evidence of traditional mechanisms proposed to explain the success of this invasive species (Table 2). According to the theoretical framework proposed by Catford et al. (2009) the interaction between propagule pressure, characteristics of *L. lucidum* and biotic and abiotic characteristics of the recipient community with the additional influence of humans contributed to the successful invasion of *L. lucidum* in different ecosystems. A particularly important mechanism to explain *L. lucidum* success emerging from this review, is its ability to deal with well-established ecophysiological trade-offs, i.e. combinations among tree traits (e.g. survival and growth; Gilbert et al. 2006). For example, a well-established trade-off in plants is between shade-tolerance, herbivory resistance on one side versus rapid growth and high seed production on the other. *L. lucidum* possess both qualities: high seed production, early reproduction and high growth rate, makes it behave as a pioneer species; but high herbivory resistance, shade tolerance, and high wood density makes it behave as a late successional species, able to compete in mature forests without disturbance (Swaine 1994; Gilbert et al. 2006; Easdale et al. 2007; Johnson 2009; Benetti 2015). Trade-offs contribute to tree species coexistence, maintenance of local diversity, and favor species in different environments and times (Gilbert et al. 2006). Thus, breaking trade-offs may represent an advantage for *L. lucidum* encroachment into different places (e.g. open fields and intact forests; Hoyos et al. 2010) and successional stages (Zamora Rivera 2016; Malizia et al. 2017).

Prevention and Control

Methods of Prevention

Given that *L. lucidum* is a prolific seed producer, prevention (i.e. restricting the use, sale, and transport of this species outside its native range) is the most effective measure to avoid impacts in areas where it has not been yet introduced (Maddox et al. 2010; Brixner Dreyer et al. 2019). Currently, some countries, where *L. lucidum* is a problem, implement preventive measures (Table 3). In other countries where *L. lucidum* also is considered invasive (i.e. Argentina, Brazil, Uruguay), there are no legal preventive measures reported up to date.

Methods of Detection

A good option to early detection at a relatively low cost are the citizen science programs designed to report and monitor invasive species by submitting observation data through websites or mobile phone applications (Pocock et al. 2017; Graham et al. 2011). Currently, there is one application that shows the *L. lucidum* distribution map in USA (Table 3). Also, the models of potential distribution (e.g. Montti et al. 2017) are a valuable tool to identify where the species can thrive once introduced.

Table 2 Empirical evidence of traditional mechanisms that explain the success of *L. lucidum* invasion

| Hypothesis | Explication | Evidence for <i>L. lucidum</i> | References |
|--|---|--|--|
| <i>Propagule pressure</i> ; (Lockwood et al. 2005) | High supply and frequency of propagules introductions increase the chance of successful invasion due to higher probability of introduction to a favorable environment. | This mechanism explains part the success of the <i>L. lucidum</i> invasion in dry and subtropical forests of Argentina. These forests experienced urban growth. Due to <i>L. lucidum</i> was used as an ornamental tree, urban areas function as propagules sources of <i>L. lucidum</i> promoting its expansion in these areas. | (Aragón and Morales 2003; Ferreras et al. 2008; Gavier-Pizarro et al. 2012; Montti et al. 2017). |
| <i>Limiting similarity</i> ; (Hiero et al. 2005) | Often the invasion success occurs when the exotic species are functionally different to native species so encounter minimal competition and can fill an empty niche. | <i>L. lucidum</i> bears fruits at a different season than its co-occurring native fleshy-fruited trees in dry forests and subtropical forests of Argentina, providing frugivores food in an otherwise resource-poor season. This difference in fruiting between <i>L. lucidum</i> and native species seems to be key to its success as an invader species. | (Grau and Aragón 2000; Ferreras et al. 2008). |
| <i>Sampling</i> (Crawley et al. 1999; Catford et al. 2009) | Interspecific competition drives invasion. Species identity is more important than species richness of the recipient community, and invasion occurs when invading species are able to exploit resources and avoid enemies more effectively than resident species. | <i>L. lucidum</i> invasion triple total tree biomass irrespective of species richness and monocultures of <i>L. lucidum</i> are more productive than any of the most species-rich, uninvaded communities in a subtropical montane forest of Argentina. | (Flombaum et al. 2017) |
| <i>Invasional meltdown</i> ; (Simberloff and Von Holle 1999) | Often there are direct or indirect facilitation relationships among invaders, where one species makes habitat or community more amenable for the other. | The exotic <i>Pyracantha angustifolia</i> exerts a facilitation effect on <i>L. lucidum</i> in the dry forest of central Argentina <i>P. angustifolia</i> offer a cool microenvironment in summer and a moist soil in the dry season reducing environmental stress enhanced survival of <i>L. lucidum</i> saplings. | (Tecco et al. 2007). |
| <i>Enemy release</i> (Keane and Crawley 2002) | Upon entry into a new range, invader loses its natural enemies that limit its population size | <i>L. lucidum</i> experience significantly less foliar damage under field conditions in the novel | (Montti et al. 2016). |

Table 2 (continued)

| Hypothesis | Explication | Evidence for <i>L. lucidum</i> | References |
|---|---|---|--|
| | in its native range. Resources previously used for defence are reallocated to growth and reproduction, thereby facilitating invasion. | (Subtropical mountain forest in Argentina) than in the native range. | |
| <i>Environmental heterogeneity</i> (Melbourne et al. 2007; Catford et al. 2009) | Habitats with high environmental variability contain a diverse array of niches that can host a variety of species. Invasion will be successful if there are an insufficient number of indigenous species to fill the available niches (i.e. indigenous species pool too small). | <i>L. lucidum</i> invaded subtropical montane regions characterized by a high environmental variability (i.e. due to the habitat heterogeneity of the mountains). | (Gavier-Pizarro et al. 2012) |
| <i>Disturbance</i> (Colautti et al. 2006; Catford et al. 2009) | Disturbance events increase resource availability and reset succession, giving invading species an equal chance of success at colonization and establishment. | <i>L. lucidum</i> colonizes forests and grasslands after disturbance and abandoned agricultural areas in many regions. | (Grau and Aragón 2000; Lichstein et al. 2004; Torres et al. 2014; Montti et al. 2017, Brazeiro 2018) |

Methods of Control

Physical Methods

Experiments of stem cutting or manual removal of *L. lucidum* were effective in different invaded areas (Table 3). However, the manual removal of *L. lucidum* seedlings would be efficient in places where there is an incipient invasion (Aslan et al. 2012; Valfré-Giorello et al. 2019). In the case of stem cut is made, it is necessary the removal of a large surface roots to prevent resprouting (Johnson 2009).

L. lucidum is susceptible to fire due to its thin bark and cambium, high water content in its tissues and lack of other fire-protective features (Swarbrick et al. 1999; Batista and Biondi 2009; Herrero et al. 2016). Thus, populations of the invasive *L. lucidum* could be reduced through application of prescribed burns in areas with a high proportion of this species and where fire is compatible with the conservation of desired components of the ecosystem (Table 3).

Chemical and Combination of Mechanical and Chemical Methods

Different herbicides and their combination with mechanical methods were tested to control the invasion of *L. lucidum* (Table 3). However, the most effective way to control *L. lucidum* appears to be a combination of chemical and mechanical techniques (McGregor 2000; Demers et al. 2012).

Table 3 Type of methods applied for the prevention, detection and control of *Ligustrum lucidum*

| Type of Methods | Application | Country | References |
|--------------------|--|---|--|
| Prevention | Selling or planting <i>L. lucidum</i> is illegal | New Zealand and some states of Australia | Queensland Government (2016) |
| | <i>L. lucidum</i> cannot be planted or must be removed and destroyed | Several southern states of USA and South Africa | Centre for Invasive Species Ecosystem Health (2016); Invasive Species South Africa (2016) |
| Detection | EDDMapS shows the <i>L. lucidum</i> distribution map and the density of records considering the literature and observation | USA | (https://www.eddmaps.org/distribution/uscounty.cfm?sub=5942), Mowatt (1981) |
| Mechanical control | Cut the stem of <i>L. lucidum</i> at a height near the ground and then covering the stump with black nylon reduced the individual's ability to regrow | Australia | Valfré-Giarello et al. (2019) |
| | Cut the stem of <i>L. lucidum</i> and apply a polyethylene bag reduced survival by 32% and regrowth height by 95% compared to untreated controls | Argentina | Ziller and de Sá Dechoum (2009) |
| | Individuals of <i>L. lucidum</i> were successfully removed manually in a protected area | Brazil | Torres et al. (2014) |
| | Fuel reduced the resprouts, seedling establishment and survival of <i>L. lucidum</i> | Argentina | Swarbrick et al. (1999) |
| | The fire can kill small trees and saplings and might also deplete the seed bank so the prescriptive fire allowed partial control of <i>L. lucidum</i> | Australia | Madden and Swarbrick (1990) |
| Chemical control | Stem injection of metsulfuron methyl is least costly (i.e., 40% cheaper than any other treatment) and is effective for controlling young plants of <i>L. lucidum</i> | Australia | Mowatt (1981) |
| | <i>L. lucidum</i> can be killed by injecting concentrated herbicide (mainly triclopyr) into the trunk without cutting the tree down | Australia | Hareiche and Brazeiro (2018) |
| | The perforation with glyphosate injection demanded more time and money than banding with manual chain and banding with glyphosate application but showed the greatest effectiveness, with an associated mortality greater than 70% | Uruguay | |

Recently, the combination of removal of *L. lucidum*, planting of native species and resprouting control in the first years after removal has been suggested as an alternative to control the *L. lucidum* invasion and restoration of native vegetation (Plaza Behr et al. 2016). Furthermore, addition of native seeds and canopy opening in *L. lucidum* forest might counteract the abiotic constraint and contribute to restoration success (Ferreras et al. 2019). In particular, planting of native fruiting species could reduce spread of *L. lucidum* seeds by creating competition for dispersers (Aslan 2011).

In line with the results of a meta-analysis on invasive plant control (Kettenring and Adams 2011), we note that all studies about control of *L. lucidum* reported here were conducted in the short term (≤ 3 years) and on a limited spatial scale (< 1000 m²) and very few studies evaluated the economic costs of control. Furthermore, to our knowledge there are no studies that have explicitly attempted to apply results from small-scale experiments to the medium-large scale ones. This type of studies is very important to make management recommendations because the recommended method (effective and monetary and logistically feasible) depends on the spatial scale of the invasion and the type of impacts to prevent or control.

Research Gaps and Priorities

Despite being perceived as an important invader, there is little research reflected in publications in countries such as Mozambique, Pakistan, Spain, Uruguay and Japan. In contrast, the species and its ecology have been more researched in Argentina, Brazil, Australia and USA, but there are still important gaps to be filled. We identified the following priority research topics on this species:

- Assessment of the “impact threshold” that is the abundance at which *L. lucidum* begins to cause substantial impacts on biodiversity, and ecosystem properties and processes. The impact threshold is known for lianas, whose communities decline when *L. lucidum* represents 25% of the total tree abundance in a subtropical montane forest of NW Argentina. Beyond this threshold, lianas decline to less than 2 species and 5 individuals in 400 m² plots (Ceballos 2019).
- Research about the physiology of the species (e.g. photosynthesis rates, xylem sap flow, architecture hydraulics); with particular focus in identifying the mechanisms by which the species withstand the r-k tradeoff and has properties of both pioneer and late successional species. Also, the evaluation of functional traits of *L. lucidum* roots (e.g. biomass, depth and metabolism) is important to understand how this species influence in the dynamics of water, carbon and nutrients.
- Establishment of permanent plots in forests invaded by *L. lucidum* to describe the dynamics of already invaded areas, and establishment permanent plots in incipiently invaded forests to monitor how the invasion of *L. lucidum* progress and its dynamics when other tree species are abundant (e.g. Malizia et al. 2017). Permanent plots provide valuable information about the persistence of the invasion across the time and help to identify useful patterns in conservation and forest management. Currently, there are permanent plots in invaded areas in a subtropical montane forest of NW Argentina (Malizia et al., unpublished data); we encourage the use of this approach in other regions.

- Assessment of the social perception of *L. lucidum* invasion could provide information for the development of education programs and local management programs by community members.
- Research about economic cost of *L. lucidum* invasion and control. In order to make management recommendations of *L. lucidum* at large scale of invasion, it is necessary that future studies provide information on the costs associated with control methods evaluated and then consider the effectiveness of application on large-scale.
- Development of early warning systems and detection/elimination of seed sources of *L. lucidum* in newly invaded habitats, based on demography models of invasion (e.g. Travis et al. 2011; Aben et al. 2016; Rodrigues et al. 2015; Powell and Araújo 2017).
- Development of restoration plans and assessment ecosystem recovery after removal or eradication of *L. lucidum* should be considered in management strategies.

Conclusions

Ligustrum lucidum can be considered a paradigmatic example of a successful invasive tree species, and as such, it merits more research as a model of a type of biological behavior likely to become more common in the Anthropocene. From the reviewed literature we highlight the following conclusions:

- 1 *L. lucidum* is a highly invasive species that may develop monodominant forest stands with high biomass, primary productivity and evapotranspiration, low biodiversity, and altered biogeochemical cycles associated to changes in decomposition and microflora.
- 2 It aggressively invades abandoned agriculture fields, but also mature native forests. It persists in the shade and has a high resprouting capacity.
- 3 Its invasive capacity is favored by its plasticity in key ecophysiological trait attributes (i.e.g. shade tolerance and high growth, high wood density, high height and high recruitment) and its capacity to overcome trade-offs, such as between colonization and competition; growth and shade tolerance, seed production, longevity and resprouting capacity.
- 4 Dispersal from urban and periurban environment to natural ecosystems is guaranteed due to abundant seed production coupled with efficient dispersal by birds, which are common in most environments. In addition, the existence of abandoned fields allows generating monodominant stands that in turn can act as secondary sources for invasion of nearby native forests.
- 5 Given these characteristics, it is very likely that this species will continue expanding its range of distribution and relative importance in native ecosystems; with potentially negative effects for biodiversity and some ecosystem services (e.g. water regulation); but positive effects in other ecosystem services (e.g. services of regulation as climate regulation and air purification, provisioning services as fuelwood and cultural services as aesthetics, recreation and ecotourism).
- 6 Since *L. lucidum* invasion is a problem in several countries, cooperation between countries, mainly between neighboring countries, is needed for the successful

implementation of management or control of this species. To prevent the negative effects of the invasion, management options at the local level should include early warning systems (e.g. development of apps to detect presence of *L. lucidum* and detection/elimination of seed sources in newly invaded habitats). Also in case that eradication is an impossible option, containing the invasion could be a good alternative. This will be possible by developing a decision-making framework for adaptive managing invasive species. This type of approach can be possible using predictive models of habitat distribution that include information about dispersal dynamics of the species and land use maps to prioritize area to control the future invasion. Particularly, the success of this management will depend on involving relevant stakeholders e.g. policy makers, from each provincial or national context and build human capacity to evaluate and monitor long-term management and control practices. Finally, management strategies should include an active plan for the restoration of native communities.

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