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RESEARCH ARTICLE

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Predicting current and future global distribution of invasive *Ligustrum lucidum* W.T. Aiton: Assessing emerging risks to biodiversity hotspots

Lía Montti[1,2,3,4] | Santiago José Elías Velazco[3,5,6] | Justin M. J. Travis[7] | H. Ricardo Grau[4,8]

[1]Instituto de Investigaciones Marinas y Costeras (IIMyC), FCEyN, Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mar del Plata, Buenos Aires, Argentina

[2]Instituto de Geología de Costas y del Cuaternario (IGCyC), FCEyN, Universidad Nacional de Mar del Plata-CIC, Mar del Plata, Buenos Aires, Argentina

[3]Instituto de Biología Subtropical (IBS), Universidad Nacional de Misiones (UNaM) – Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Misiones, Argentina

[4]Instituto de Ecología Regional (IER), Universidad Nacional de Tucumán (UNT) – Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Tucumán, Argentina

[5]Department of Botany and Plant Sciences, University of California – Riverside, Riverside, CA, USA

[6]Programa de Pós-Graduação em Biodiversidade Neotropical, Universidade Federal da Integração Latino-Americana (UNILA), Foz do Iguaçu, Brazil

[7]School of Biological Sciences, University of Aberdeen, Aberdeen, UK

[8]Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán (UNT), Tucumán, Argentina

Correspondence
Justin M. J. Travis, School of Biological Sciences, University of Aberdeen, Aberdeen AB242TZ, UK.
Email: justin.travis@abdn.ac.uk

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Abstract

Aim: Biological invasions represent one of the main anthropogenic drivers of global change with a substantial impact on biodiversity. This impact can be particularly acute in biodiversity hotspots. *Ligustrum lucidum* W.T. Aiton is a tree species native of China that, from as early as the eighteenth century, has been introduced broadly around the globe, becoming a serious invasive species. We aim to predict *L. lucidum's* current and future potential distributions at a global scale and assess the degree to which biodiversity hotspots are at risk of invasion.

Location: All continents.

Methods: Using global presence data, climatic and edaphic variables, we developed an ensemble model to predict current and future periods (2050 and 2080) global distribution of *L. lucidum*. Susceptible countries and hotspots of biodiversity were identified.

Results: Important regions within China and neighbouring countries are likely to be environmentally suitable, but they are not currently occupied. Biodiversity hotspots in South America are highlighted as being at current risk of invasion. Notably, climate change may increase risks across large extents of biodiversity hotspots, mainly in South America and Africa, especially by 2080 period.

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Main conclusions: Current and future potential distribution of *L. lucidum* overlaps with biodiversity hotspots worldwide. Control of *L. lucidum* is a challenge once established. Thus, species distribution modelling helps to identify risk areas, guiding their early detection in current or future suitable areas. Our findings can be useful as a guide to develop region-specific invasion management strategies to prevent and/or control this species' spread.

KEYWORDS
biodiversity threat, biological invasion, ecological forecast, ensemble models, glossy privet, species distribution models

1 | INTRODUCTION

Invasive alien species (IAS) are one of the five direct drivers of global biodiversity loss (IPBES, 2019). Predicting their expansion under different scenarios is paramount for designing and implementing active surveillance and management actions (Essl et al., 2011; Roy et al., 2014). Human agency plays a critical role in their distribution (Vaz, 2018). Nevertheless, in the case of invasive plants, climate, soil properties and dispersal capacity are three of the most important determinants and constraints to their distribution (Dupin & Smith, 2019; Figueiredo et al., 2017; Liao et al., 2020). Some invasive plants can be limited to growing in areas with similar climatic conditions as in their native range (Peterson, 2003; Petitpierre et al., 2012; Wiens & Grahams, 2005). However, during an invasion process, other species may additionally expand into regions exposed to different climate conditions than they experience in their native range (Atwater et al., 2018; Broennimann et al., 2007; Gallagher et al., 2010; Goncalves et al., 2014). This characteristic of many invasive plants provides a particular challenge in predicting suitable regions for the species under current or future climate conditions.

Glossy privet (*Ligustrum lucidum* W.T. Aiton, Oleaceae) is a highly invasive tree species present on all continents except Antarctica (Fernandez et al., 2020). The species' original distributional range is thought to have been constrained to the centre-west of China, including Yunnan, Guizhou, Sichuan and Hunan provinces (De Juana, 2009). However, due to dispersal events and long-standing and diverse human uses, the species occurs currently among a broader range of edaphic and climatic conditions along the southern half of China (Chang & Miao, 1986; Editorial Committee of Flora of China CAS, 1999; Wilcox, 2000). Outside its native area, *L. lucidum* has been introduced around the World, firstly into the United Kingdom by European horticulturalists in 1794, and since then, it has been widely used as an ornamental in Europe (Chittenden, 1951). The species' introduction was commonly associated with ornamental purposes (CABI, 2020; Hummel et al., 2014; Johnson, 2009; Rodrigues et al., 2015). However, more complex historical and socioeconomic causes, as human migrations and/or trade between the donor area of propagules and the receiving areas, could also have played an important role in *L. lucidum's* distribution (Madelón et al., 2021; Montti et al., 2017).

To date, scientific research on *L. lucidum* has mainly focused on its biology and functional traits (Aguirre-Acosta et al., 2014; Aragón et al., 2014; Montti et al., 2016). There has been a particular focus on the species' negative impacts, including a severe decrease in native biodiversity (Ayup et al., 2014; Ceballos et al., 2015; Ferreras et al., 2015; Furey et al., 2014; Malizia et al., 2017) and changes on environmental variables such as reduction in soil humidity and light availability affecting nutrient cycling (Aragón et al., 2014; Whitworth-Hulse, 2018; Zamora Nazca et al., 2014). Further work has investigated the species' role in fostering human allergic diseases (Robledo-Retana et al., 2020). Most importantly, in terms of projecting regions that are likely to be suitable for the species, it was recently demonstrated that invasive populations have expanded into warmer and wetter climatic conditions than native ones (Dreyer et al., 2019).

In recent years, there has been growing recognition of the particular risks that invasive species may pose for biodiversity hotspots and protected areas (Bellard et al., 2014; Li et al., 2016; Liu et al., 2020). Thirty-five biodiversity hotspots have been defined based upon the high levels of species richness and endemism that they possess (Mittermeier et al., 2004). Together, these areas contain over 75% of the World's vertebrate species and over 50% of the World's plant species. Thus, these biodiversity hotspots are a clear priority for conservation actions, and there are indications from recent work that these regions may be disproportionately at risk from invasive species (Li et al., 2016). Given the dramatic impact that *L. lucidum* can have on the ecosystems it invades, including dense monodominant stands, it is important to assess the possibility it has to invade these biodiversity hotspots under current and future projected conditions.

Because *L. lucidum* is an invasive species, promoted mainly as an ornamental plant, identifying areas that could be environmentally suitable for the species is a priority for developing early detection networks, control strategies and trade regulations. However, studies on global distribution, habitat suitability or how future climate change can impact the species' potential distribution are still lacking. Species distribution models (SDMs), which aim to predict environmental suitability by linking species distribution data with

environmental data, have been extensively used for different species (Guisan et al., 2017; Thuiller et al., 2019; Zhang et al., 2019). Thus, here we aim to answer the following questions: (a) In which countries is *L. lucidum* present, and what is the current potential distribution based on climatic and edaphic variables? (b) Which areas of the World could, in future climatic conditions, exhibit suitable environment conditions? and (c) What is the current and future susceptibility of the biodiversity hotspots to be invaded?

2 | METHODS

2.1 | Data collection and curation

A total of 5,822 presence records were collated from a large number of herbarium specimen data from twenty-six Herbariums in six countries (Herbarium List. Table S1). Additionally, many records were gained across a range of sources such as the Global Biodiversity Information Facility (GBIF; http://www.gbif.org accessed on April 2019, https://doi.org/10.15468/dl.dshsxz), Tropicos (http://www.tropicos.org/ accessed on March 2019), The Inter-American Biodiversity Information Network (IABIN; http://www.inbiar.uns.edu.ar/, http://www.institutohorus.org.br/iabin/i3n/ accessed on March 2019) and Global Invasive Species Database (http://www.iucngisd.org/gisd/). We also used records from published literature (i.e. Gavier-Pizarro et al., 2012; Hoyos et al. 2010; Presutti, 2011) and extensive personal observations made by L. Montti, N. Acosta-Aguirre, C. Fagúndez, M. Ayup, K. Garcia and S. Pacheco.

Records in native or novel areas were checked by screening available literature and by consulting with botanical experts. Records curation consisted of exhaustive revision and excluding records where information was considered unreliable, including potential misidentified specimens. We also excluded erroneous records (e.g. coordinates outside the studied area under which they had been listed, records located in the sea), and duplicates resulting from the merger of records from different sources. Furthermore, we excluded records with coordinates without decimals or with half-degree decimals (i.e. 0.5), georeferenced in the countries or states centroid, capitals or institutions. The native/invasive status in each country was classified according to literature and botanical expert consultation. After this process was completed, we ended up with 1,959 presence records.

Species' records are frequently over-represented in highways, urban areas, and protected areas, among others (Mccarthy et al., 2012; Meyer et al., 2016), and this has the potential to reduce a models' quality (Beck et al., 2014) if it is not accounted for. We chose to correct this records sampling bias by using environmental filters. This method consists of creating a regular grid that divides the environmental space and then filters the records by the random selection of one occurrence within each grid-cell (Varela et al., 2014). An alternative is to use spatial filters (i.e. performed in the geographical space), but this has been demonstrated to be less efficient than the environmental one (Castellanos et al., 2019). We used an environmental filtering protocol adapted from Velazco et al. (2020). This consisted of performing a principal component analysis with environmental variables (see environmental variable section) and used the first three principal components to describe environmental space where occurrences will be filtered. Then, regular grids were created in this multivariate space with different cell sizes. The cell size is determined by the number of bins where each variable range is divided (Castellanos et al., 2019). There is a trade-off between the number of bins and the number of filtered records because as the number of bins decreases, the cell size of the grids increases, and the number of filtered records decreases (Castellanos et al., 2019). In order to access the optimum number of bins, we tested five number of bins between 10 and 50. For each one, we calculated the spatial autocorrelation among filtered records based on Moran's I (Moran, 1948) and the number of filtered records. Then, we selected the set of bins with the lower quartile of the Moran's I and, of these, the one with the highest number of records (Velazco et al., 2020). The best number of bins was 50, which had a mean Moran's I of predictors of 0.447. Finally, we obtained 957 cleaned and unbiased records, which were used to construct species distribution models.

2.2 | Environmental variables

We chose to use climatic and edaphic variables to create SDMs because their combination has been demonstrated to increase model performance for plants (Bertrand et al., 2012; Thuiller, 2013; Velazco et al., 2017). We used 19 bioclimatic variables for current period (1979–2013) and two periods, 2050 (2041–2060) and 2080 (2061–2080), for future climate conditions available in the Chelsa v1.2 database with 30 arc-sec resolution (~1km at the equator; Karger et al., 2017). CHELSA future climate data use a delta change method by B-spline interpolation of anomalies (deltas) to correct data bias (Karger et al., 2017). For edaphic data, we used six physical soil properties provided by the SoilGrids with 30 arc-sec resolution (Table S2; Hengl et al., 2017). We selected these variables, assuming they are more stable through time than those related to chemical edaphic properties (like carbon stock or pH). Climatic and edaphic variables were upscaled by calculating their mean at 0.2 degrees resolution (~22 × 22 km).

Because knowing the geographical distribution of the species projected under future climate scenarios can help guide risk management strategies, we evaluated the potential invasion assuming two Representative Concentration Pathways, RCP 4.5 (moderate emission scenario) and a pessimistic emission scenario RCP 8.5 (IPCC, 2013; Meinshausen et al., 2011). The RCP 4.5 assumes the imposition of emissions mitigation policies, with moderate global emissions of greenhouse gases and land-uses, which stabilize radiative forcing at 4.5 W/m^2 (approximately 650 ppm CO_2-equivalent) and global mean surface temperature exceeding 1°C by 2,100 (Thomson et al., 2011). The RCP 8.5 represents one of a suite of scenarios that describe the highest greenhouse gas emissions combined with a high population and relatively slow income growth, with modest rates of technological change and energy intensity improvements

(Riahi et al., 2011). The RCP 8.5 delivers a global mean surface temperature increase of about 4.3°C by 2,100, relative to pre-industrial temperatures, a potentially extreme future situation likely resulting from society's failure to take low efforts to reduce greenhouse gas emissions (UNEP, 2017). We used multiple Atmosphere-Ocean General Circulation Models (AOGCMs) in order to account for variability driven by RCP 4.5 and 8.5 projections. We used the AOGCMs: CSM4, HadGEM2-OA, IPSL-CM5-LR, and MIROC-ESM-CHEM from the Fifth Assessment of the Intergovernmental Panel for Climate Change (1km^2 resolution; IPCC, 2013).

To avoid multicollinearity and reduce the number of environmental variables used in the models, we used the derived variables from a principal component analysis (PCA). This PCA was performed based on the correlation matrix of the environmental variables for the current condition. Then, we used the eigenvectors originating from each principal component to calculate the scores for each grid-cell for both current and future conditions (i.e. each AOGCM and RCP). We used the nine principal component axes, which explained >95% of the total variance (Table S3; De Marco & Nóbrega, 2018).

2.3 | Species distribution models

The choice of algorithms is the primary source of uncertainty for current and future projected distributions generated by SDMs (Thuiller et al., 2019). To account for and explore this source of uncertainty, we used four different algorithms: Random Forests (RF, Liaw & Wiener, 2002), Support Vector Machine (SVM, Karatzoglou et al., 2004), Maximum Entropy (Maxent, Phillips et al., 2017b) and Gaussian Process (GAU, Golding & Purse, 2016). For RF, the model was tuned automatically using the 'tuneRF' function of the *randomForest* R package (Liaw & Wiener, 2002) based on the improvement of the out-of-bag error parameter; thus, the best model used a mtry parameter equal to three (i.e. number of variables randomly sampled as candidates at each split). RF was performed with default values of the step factor, 500 trees. SVM was performed with a radial basis kernel, with a constant cost value equal to one, and based on probabilities classes. We employed an inhomogeneous Poisson process procedure (Phillips et al., 2017b) to Maxent fitting. We used linear, quadratic, product and hinge features, default regularization values, 10,000 background points and clog-log output format. The Gaussian Process (GAU) models were constructed using a Laplace approximation (Golding, 2014). For RF, SVM and GAU, we randomly created pseudo-absences distributed 50 km distant to each presence, resulting in a number of pseudo-absences equal to the number of presences (Barbet-Massin et al., 2012). We used Terrestrial Ecoregions of the World (Olson et al., 2001), where *L. lucidum* was recorded to constrain the area used to construct SDMs, that is the area where pseudo-absences and background points were located.

We used presence records from native and invaded regions together to create SDMs. Recently, it was reported that this species might be experiencing a climatic realized niche shift in the course of the invasion process (Dreyer et al., 2019). This indicates the non-equilibrium of species niche and the possibility that the fundamental niche may not be represented adequately only in the native region (Andrade et al., 2019). *Ligustrum lucidum* is easily transported by humans, and as we mainly focus on predicting the areas susceptible to its invasion, we estimated habitat suitability and interpreted results assuming no limitations to their future dispersal. Hence, the use of native and novel areas pooled provides the best option (Beaumont et al., 2009; Broennimann & Guisan, 2008; Zhang et al., 2020). Because we are also interested in projecting this model to a worldwide scale, we evaluated model performance using spatial block cross-validation because it controls for the potential spatial autocorrelation between training and testing data and evaluates model transferability more appropriately than other partitioning methods (Roberts et al., 2017). To select the best grid size (Figure S1), we generated 20 grids with resolutions ranging from 0.5 to 10 degrees and selected the one with (a) the lowest spatial autocorrelation, (b) the maximum environmental similarity and (c) the minimum difference of numbers' records between training and testing data (Velazco et al., 2019). The optimum selected grid had a grid size of 9.5 degrees, a Moran's I of 0,168, a MESS of 14.965 and a standard deviation between the number of occurrences between partitions of 0.181. It is prudent to validate SDMs performance based on multiple evaluation metrics (Sofaer et al., 2019) because they can be variable regarding their threshold dependence (Liu et al., 2009) and sensitivity to prevalence (Leroy et al., 2018). Therefore, we used the metrics Area Under the Curve (AUC), True Skill Statistic (TSS), Jaccard, Sørensen, F-measure on presence-background data (Fpb), and the Boyce Index (Allouche et al., 2006; Leroy et al., 2018). We used a threshold that maximized Sørensen and Jaccard metrics to calculate threshold-dependent metrics (i.e. TSS, Jaccard, Sørensen and Fpb). The final model was constructed performing a PCA with the suitability estimation of the four algorithms both for current and future conditions. We used this ensemble approach because it reduces uncertainty derived from individual models (Zhu & Peterson, 2017). The ensemble was based on a PCA of suitability values predicted by each algorithm. The eigenvector of the first principal component was used to calculate the scores used as values of suitability. This ensemble model was binarized by a threshold that maximized Sørensen and Jaccard metrics (0.426) because it showed the maximum sensitivity value (0.936).

Because we constrained the area used to construct models and we aimed to perform global and future projections, it is likely that our models will estimate suitability values for out-of-range environmental conditions used to fit them (model extrapolation). We evaluated model extrapolation for both current and future conditions based on the Mobility-Oriented Parity (MOP) approach (Owens et al., 2013). This approach calculates the mean Euclidian distances between the environmental condition of a given point where a model will be projected and each point of the calibration area (Owens et al., 2013). One characteristic of MOP is it allows to restrict the proportion of the nearest portion of the cloud of calibration area used for calculation (we used 10% of the cloud of calibration area). Current and future species' ranges were constrained with a very conservative

threshold assuming as potential invasion only those cells with MOP values ≥0.9 (Figure S4). We used the standard deviation of different algorithms and AOGCMs as future models' uncertainty.

Data processing, models and figures were performed with R software v3.6.1 (R Core Team, 2019); the R packages 'raster' (Hijmans, 2017) was used to handle spatial data and 'CoordinateCleaner' (Zizka et al., 2019) in conjunction with our own scripts, was used to perform records cleaning and sampling correction bias. We used the 'ENMTML' R package to create, evaluate and project SDMs (Andrade et al., 2020). We used the 'randomForest' (Paradis et al., 2004), 'kernlab' (Karatzoglou et al., 2004), 'GRaF' (Golding, 2014) and 'maxnet' (Phillips, 2017a) packages to fit RF, SVM, GAU and Maxent models, respectively. We used goode homolosine projection (EPSG 8,802) to estimate the surface extent of suitable areas with a grid-cell resolution of 22 × 22 km. All analyses and computed descriptive statistics were conducted using Spatial Analysis tools from ArcGis 10.1 and R v3.6.1 (R Core Team, 2019). To evaluate invasion risk and susceptibility to invasion in global priority biodiversity conservation areas, we focused our analyses using the Mittermeier et al. (2004) classification of biodiversity hotspots.

3 | RESULTS

3.1 | Global map based on presence records

Historical evidence from herbarium catalogues revealed that earlier itemized species records outside its native range were documented since the middle of 1,800. The number of records per year increased rapidly after 2000. *Ligustrum lucidum* started to be methodically registered later in Oceania compared with Europe and America, but today this continent presents the highest number of records. Africa was the continent where the species was later recorded and currently provides fewer records (Figure 1). Australia, New Zealand, United States of America, Mexico, Brazil, Argentina, Uruguay, Bolivia, Spain and South Africa have either declared the status of this species as 'invasive' or have considered it problematic for natural ecosystems (Table 1). However, in several countries around the World (e.g. Norway, Belize, Costa Rica, Colombia, Venezuela, Ecuador, Guatemala, Mali, India, Russia, Italy, Portugal, France, United Kingdom, Turkey, Georgia or Pakistan), the species has been introduced but is not considered a problem or not information about its status was declared yet (Figure 1, Table 2).

3.2 | Current potential distribution

The final ensemble model had a Boyce and Fpb metric higher than individual models indicating good performance in predicting the suitable area for the species (Table S4). The potential current distribution (i.e. potentially invadable) of *L. lucidum* around the globe is 14,201,846 km^2, an area slightly smaller than the size of South America (17 million km^2; Figure 2). In China, the species has a broad potential distribution, with more than 2,489,214 km^2 of suitable environmental conditions. However, the centre and south of the country appeared to be the most suitable area, as are neighbouring regions within Laos and Myanmar. In the rest of Asia, southern parts of Japan and Korea present regions of environmental suitability too, and, consistent with this *L. lucidum* has been declared as a problem for native ecosystems in these countries (Table 1). Our model indicates that other areas of this continent, such as the Himalayan slopes of India, Bhutan, Nepal and Pakistan, and the moister sectors of Iran and Turkey, also present suitable conditions (Table 2 and Figure 2). However, either information on presence is not available for these regions, or records are very scarce. Neither, records of invasion cases or negative effects in their natural ecosystems.

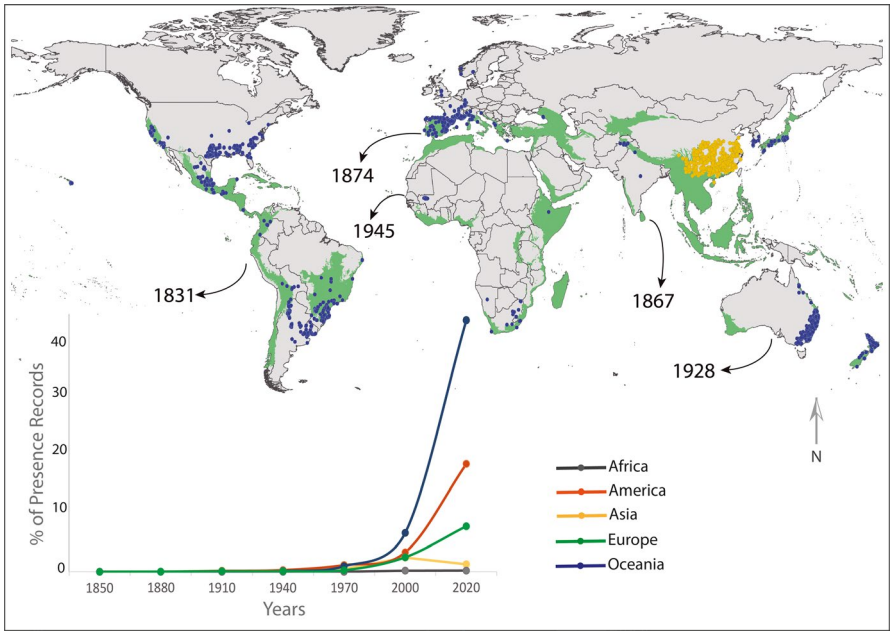


FIGURE 1 Global map of *Ligustrum lucidum* built using reliable presence records (yellow dots represent native region and blue dots novel region records). The first georeferenced specimen per continent is pointed out with an arrow (GBIF, catalogue numbers 1804344, 120859, P00392942, 1258773163, 412401 according to chronological order). The plot at the bottom depicts the percentage of presence records per continent over time, and green areas show the high biodiversity hotspots (Mittermeier et al., 2004)

TABLE 1 Countries where *Ligustrum lucidum* is considered as an invasive species and its current and future potential distribution assuming a RCP 8.5

Invaded country	Source that declared	Current	Future 2050	Future 2080
Argentina	I3N Argentina; Fernandez et al., 2020	899,260	752,001 +40,679; −187,938	618,970 +29,100; −192,709
Australia	GISD, 2019; Wilcox, 2000	1,064,863	653,948 +18,346; −429,262	517,002 + 13,670; −430,916
Bolivia[a]	Blatnik, 2014	170,894	184,914 +61,755; −47,734	187,598 + 88,550; −104,520
Brazil[a]	I3N Brazil; Guilhermetti et al., 2013	744,694	773,731 +194,887; −165,850	1,022,153 +382,155; −129,995
Japan[a]	Csurhes & Edwards, 1998	186,304	238,446 +62,612, −10,470	122,013 +1,248; −11,315
Mexico	Davidse et al., 2009; Nesom, 2009	250,184	105,899 +8,295; −152,580	86,521 +1,892; −20,999
New Zealand[a]	GISD, 2019	131,973	156,250 +24,276; −0	153,497 + 21,523; −1,800
South Africa	CABI, 2020; Csurhes & Edwards, 1998; Invasive Species South Africa	215,582	150,615 +418; −65,385	77,678 +0; −65,385
Spain	Sanz Elorza et al., 2004; Basnou et al., 2015	496,028	319,147 +4,051; −180,932	142,759 + 5,504; −183,544
United States	GISD, 2019; Swearingen & Bargeron, 2016	1,234,981	1,328,863 +310,667; −216,785	473,191 +10,658; −866,447
Uruguay[a]	Brazeiro, 2018; Database of Biological invasions in Uruguay	174,773	174,773; +0; −0	170,245 +0; −4,528

Note: Details about gain (+) and lost (−) are showed in km^2 approx.

[a]Countries where is expected a stable or increase of potential distribution area. Current (1979–2013), Future 2050 (2041–2060) and 2080 (2061–2080) periods.

Outside of Asia, the model indicates that substantial regions are likely to provide suitable environmental conditions. In many of these regions, the presence of *L. lucidum* was recorded and even documented as a problematic invasive species. In South America, these areas include the humid slopes of the tropical Andes and the lowlands of Argentina, Uruguay, Brazil and Paraguay. In Oceania, southern Australia, and almost all of New Zealand show high suitability (Figure 2, Table 1). The same is true for South Africa and Spain in Africa and Europe, respectively.

The model also identified regions where *L. lucidum* is not known to occur currently, but will likely find suitable environmental conditions in the future. Regions predicted as currently potentially suitable for the species exist in parts of Africa (Madagascar, Marruecos, Argelia, Congo, Ethiopia and Sudan); in North America (western Canada), South America (extensive parts of the Andean region), and in large areas within Europe (Italy, France, Greece, Portugal and British isles) (Figure 2, Table 2).

Notably, the potential distribution of *L. lucidum* under current climatic conditions (Figure 2) overlaps with regions of high biodiversity wilderness areas, including Grasslands (e.g. Pampas), Savannas, Dry forest (e.g. Chaco Serrano) and major Tropical and Subtropical forest in America and Africa (e.g. Amazonia, Congo Forest, Temperate broadleaf and mixed forest; Figure 5). Among hotspots of biodiversity in the Mediterranean Basin, the Atlantic Forest, the Tropical Andean Forest, Indo-Burma and the Eastern Afromontane present the most extensive and suitable environmental current conditions for *L. lucidum* establishment and potential invasion (Figure 5).

3.3 | Potential distribution under climate change

Due to uncertainties of future climate change (Meinshausen et al., 2011), we apply a precautionary approach and focus primarily on the potential worst-case outcomes (RCP 8.5) in the main text. Results about the moderate scenario (RCP 4.5) are fully detailed in the in Supporting Information section. Our projections for 2050 and 2080 based on both RPC scenarios indicated a reduction in the total suitable area with the exception of RCP4.5 scenario during the 2050s (Tables 1, 2 and Tables S5 and S6). Under RCP 4.5 scenario from the current period, it is expected a 22.5% of expansion during 2050 and a reduction of 4% in 2080 periods (17,408 and 13,626 km^2, respectively) (Figure S2 and S3). Under the worst-case emissions outcomes (RCP 8.5) by 2050s, there will be an overall reduction of 4% in the total suitable area compared to current conditions, and this reduction may increase to 25% by 2080s. The total suitable areas projected to be available are 13,631,660 and 10,631,660 km^2 for 2050 and 2080 periods, respectively (Figures 3 and 4).

TABLE 2 List of countries with current and future potential distribution of *Ligustrum lucidum* >10,000 km^2 assuming a RCP 8.5

Invasion risk countries	Current	Future 2050	Future 2080
Nepal	10,828	2,573	868
Israel	11,683	7,065	7,069
Georgia	11,702	12,401	364
New Caledonia[a]	13,764	15,597	16,053
Indonesia[a]	14,221	47,586	90,864
Papua New Guinea[a]	15,114	54,134	82,974
Bosnia and Herzegovina	16,041	17,596	1,799
Rwanda[a]	16,730	9,350	17,223
Haiti[a]	17,697	19,565	24,226
Cuba[a]	20,129	19,247	32,055
Guatemala[a]	20,443	27,574	27,579
Libya	22,444	9,547	7,883
Philippines[a]	22,751	47,917	68,705
Croatia	23,239	32,246	11,702
Lesotho	23,995	13,303	860
Republic of the Congo[a]	24,115	127,473	125,018
Albania	27,139	17,845	12,321
Dominican Republic[a]	27,482	32,611	39,595
Chile[a]	29,095	28,807	39,487
Tanzania	32,809	27,023	22,123
Honduras[a]	33,794	43,807	40,946
Uganda[a]	33,969	91,556	130,938
Russia	35,378	94,208	8,256
Tunisia	36,543	27,347	15,400
Sweden	36,626	40,980	5,777
Venezuela[a]	36,952	80,779	108,033
Norway	38,133	49,594	8,193
Pakistan	48,828	24,347	2,039
Canada	50,198	41,765	2,107
Azerbaijan	50,517	51,536	4,481
Ireland[a]	56,187	60,865	64,099
Syria	56,356	20,950	7,663
South Korea	59,531	74,957	23,354
India	60,097	18,486	6,678
Ecuador[a]	60,490	70,823	87,560
Kenya[a]	64,982	88,611	107,320
Colombia[a]	67,080	123,999	148,965
Myanmar	85,457	17,147	40,852
Laos[a]	89,250	62,884	74,884
Portugal	90,027	78,850	74,010
Democratic Republic of the Congo[a]	96,409	420,783	564,539
Madagascar[a]	99,525	86,224	105,290
Vietnam[a]	118,403	91,400	119,436
Greece	126,580	91,966	35,204
United Kingdom[a]	133,641	188,558	136,781
Ethiopia[a]	142,216	130,271	143,333
Algeria	147,906	69,193	21,385
Morocco	168,381	77,638	55,499
Paraguay[a]	169,498	140,581	161,364
Iran	183,127	36,924	9,488
Peru[a]	187,543	475,359	515,445
Italy	259,101	260,856	149,395
France	290,210	343,476	124,384
Turkey	646,816	175,336	56,564

Note: Countries with potential distribution and presence records but have little awareness of invasion risk are highlighted in orange. Countries with potential distribution without presence records are highlighted in grey.

[a]Countries where is expected a stable potential distribution area or increase of it under future environmental conditions. Current (1979–2013), Future 2050 (2041–2060) and 2080 (2061–2080) periods. Countries were sort in the first column according to the current increasing surface.

For the native region, a decrease of 20% of the suitable area from the current 2,489 km^2 is expected in the future under both RCP scenarios. However, the spatial distribution of suitable environmental conditions under extreme climate changes (RCP 8.5) scenario in most invaded countries (Table 1) and countries under current potential invasion risk but not invaded yet (Table 2), would likely experience a reduction compared to current climate conditions. Stable areas were observed in some countries, including Uruguay and New Zealand. However, the potential suitable area would increase in other countries such as Brazil and Republic of Congo, where high biodiversity wilderness areas as Amazonian or Congo forest are distributed (Figure 5). A similar pattern happens under RCP 4.5 scenario (see Supporting Information section). However, tropical and mountain countries as Brazil, Papua New Guinea, Indonesia, Malaysia, Peru, Chile, Venezuela, Colombia, among others, show an increment in their future suitable areas under RCP 4.5 than in RCP 8.5 in the same period (Table S5 and S6, Figure S3).

In the other hotspots of biodiversity (Figure 5), a decrease of suitable area is projected under RCP 8.5 scenario. This is the case for Iran-Anatolian, the Mediterranean Basin and the Caucasus. Stable areas would be expected mainly in Atlantic Forest, Indo-Burma, Forest of East Australia, Madagascar and the Indian Ocean Islands. Notably, climate change may increase the potential distribution of suitable areas and thus increase the risk for invasion in the Tropical Andes and Eastern Afromontane, two of the most biodiverse and endangered regions of the world (Figure 5). A similar pattern was observed under RCP 4.5 (Figure S5).

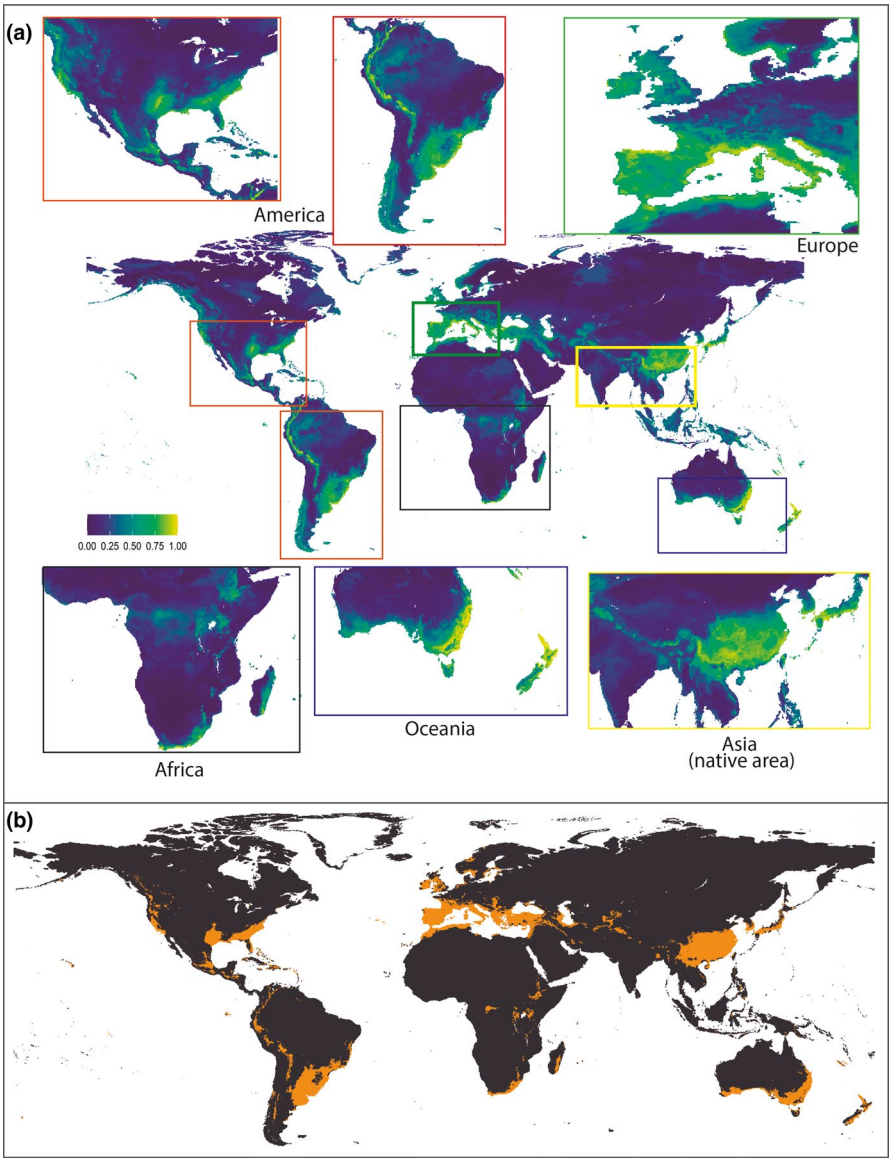


FIGURE 2 Continuous (a) and binary (b) current potential distribution of *Ligustrum lucidum* based on an ensemble of four algorithms. Grid-cells for which potential distribution was determined to be model extrapolation were eliminated based on MOP analysis in the binary map. Habitat suitability in panel range from 0 to 1

4 | DISCUSSION

We modelled the current and future potential distribution of *L. lucidum* at a global scale using a comprehensive records database from native and novel ranges. We showed that the suitable environment presents an extensive geographical distribution, which includes regions where the species is not currently known to be present or invading. While we find differences in the total suitable area between both RCP scenarios (overall reduction under RPC 8.5 and an increment under RCP 4.5), we identify regions that are consistently projected to become newly suitable regardless of the scenario modelled. Notably, some of the regions found to be currently suitable but not yet occupied, and some of the regions projected to become newly suitable under climate change overlap with important hotspots of biodiversity.

Based on the records available, we found that *L. lucidum* is already globally widespread. However, we also highlighted that the efforts and attention to record its early introduction and their impacts have been heterogeneous through time and among countries. Today, information is still incomplete, including in countries with high suitability areas (Table 2). As has been reported to occur for other invasive species (Shackleton et al., 2019), the perception of the problem, if it exists, can depend not only on ecological criteria but also on the social and economic circumstances present within a country and, in particular, as a function of the research resources available for environmental science within a country. Consistent with this, we observed that developed countries such as the United States, Australia or New Zealand, presented the most complete records of *L. lucidum* and in case of invasion detected today, they have a strong capacity to research and manage the species invasion (Early et al., 2016) with good national conservation plans in place. In contrast, in other regions, including across large parts of Africa and America that our modelling suggests are likely to be suitable for the species, there is a paucity of invasion. While this may reflect a lack of invasion by *L. lucidum* to date, it may also be due to a lack of recording and research.

Our model predictions for suitable environmental outside of the native range are largely consistent with the species' current global

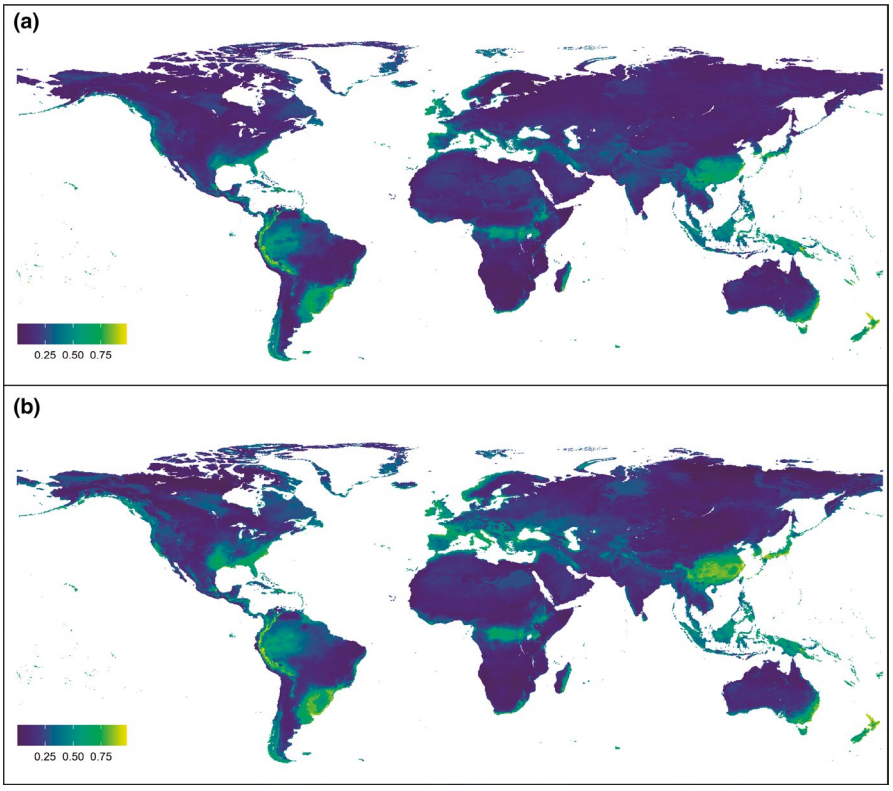


FIGURE 3 Future suitability pattern of *Ligustrum lucidum* for the periods 2050 (a) and 2080 (b) assuming a RCP 8.5. These models were based on the ensemble of four algorithms and five AOGCMs. Habitat suitability in panel range from 0 to 1

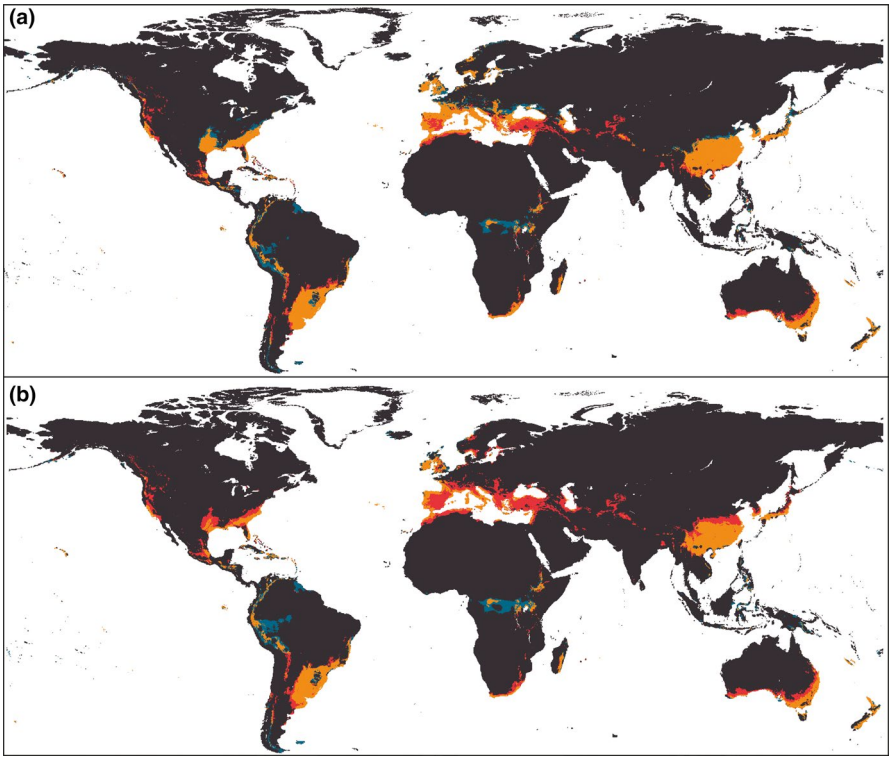


FIGURE 4 Change in suitability pattern of *Ligustrum lucidum* for the 2050 (a) and 2080 periods (b) assuming a RCP 8.5. Colours depict different types of distribution changes regarding current conditions, orange: stable areas, red: potential distribution lost, blue: potential distribution gains. Grid-cells considered as model extrapolation were eliminated based on MOP analysis in future suitability projection

distribution records (Figure 1). This was expected given that we constructed our model using presence data from native and non-native ranges. However, importantly, the predicted potential distribution is wider than the present distribution of the species. This may suggest that the invasion by *L. lucidum* has not yet achieved its full expansion range. Notably, the model indicates areas, such as the Andes and the Himalayas slopes, which are at risk of a potential invasion. In contrast, the model also identifies some environmentally suitable regions where we know that *L. lucidum* has been introduced and have not yet reported any invasion (e.g. Italy, the United Kingdom and Guatemala). While it might be that a subtle environmental factor that we did not incorporate in the model accounts for this, it could also be



FIGURE 5 Potential distribution for *Ligustrum lucidum* (km^2) among high biodiversity hotspots for current (1979–2013) and future periods 2050 (2041–2060), 2080 (2061–2080) environmental conditions for the RCP 8.5

that other abiotic or biotic factors present in these regions restrict the ability of the species to naturalize and spread.

Ligustrum lucidum tends to grow mainly in warm temperate macroclimate and has expanded its invasion range towards wet tropical areas (Dreyer et al., 2019). However, future alteration of climatic patterns could influence its distribution, as has been predicted to occur with other invasive plants (Hellmann et al., 2008). Although the projections of species distributions were developed under unavoidable simplified assumptions and uncertainties, they indicate potential challenges for *L. lucidum*. Our model projections suggest that climate change is likely to substantially affect the extent and location of suitable areas. For the native range, the current distribution is extensive, and the main suitable region is in the central and southern area of China, where humid subtropical climate conditions are predominant. Notably, the model projects a contraction in suitable area within this region in the future under both RCP scenarios. This, in addition to natural habitat fragmentation and possible loss of haplotypes diversity (Madelón et al., 2021), can have a potentially negative effect on *L. lucidum* in its native range. Interestingly, the invaded areas could potentially protect the species and its genetic diversity.

Outside of the species' native range, the model projects that some regions will decline in suitability, while others will increase; this can be important in identifying those regions most at risk from

invasion in the future. Based on the worst scenario (RCP 8.5) our models predict a reduction in potentially suitable areas in much of the south-east of Europe, America and Oceania. This would suggest a reduced invasion risk from these areas, and especially in the areas where the species has been known to be present for a substantial period without already invading, it would seem unlikely that it will become newly invasive. However, there are regions elsewhere where there is a substantial increase in projected suitable areas resulting in an increased risk of invasion. An expansion of highly and moderately suitable areas occurs in countries including Brazil, Mexico, Venezuela, Peru, Colombia, Congo and Kenya. These regions coincide with areas of high biodiversity such as Amazonas and Congo forests or with important hotspots of biodiversity, particularly Tropical Andean Forest and Afromontane. Unfortunately, such regions have relatively poor inventories of non-native species' presence, which is reflected in the data availability for *L. lucidum*. Future work is urgently needed to establish whether *L. lucidum* has been introduced into these regions. Ideally, we would recommend that, if there were isolated introductions in these areas that are projected to become suitable, removal should happen as soon as possible to decrease the species naturalization opportunity.

Although environmental species distribution models play a crucial role in predicting species' potential distribution (Andrade et al., 2019), we recognize that our predictions could be limited due to multiple uncertainties related to invasive species. A particular concern in using SDMs to project the potential distributions of invasive species is the recognition that climate niche shifts can occur during the process of invasion (Early & Sax, 2014; Medley, 2010; Parravicini et al., 2015). Thus, the spatial extent projected to be suitable for an invasive species may be substantially underestimated. We considered this issue in how we constructed the SDMs. *Ligustrum lucidum* has a relatively long history as an invasive and has been introduced to multiple regions worldwide. By building our SDMs from presence data from native and non-native regions, we have projected much broader regions of suitable space for the species than would have used only data from the species' native range. It is interesting that for China and some parts of Asia, to which it is native, when we project suitability based upon the model constructed with global data, we identify substantial regions as being suitable that the species does not currently occur within. It is likely that it was previously present in some of these regions, but it no longer occurs due to habitat loss and exploitation. However, we suggest that in other parts of China its realized niche may be substantially smaller than its fundamental niche due to competition from or predation by native flora and fauna. Outside of China, enemy release (Keane & Crawley, 2002) may be enabling the species to realize a higher proportion of its fundamental niche. The degree to which that occurs likely depends upon the local flora and fauna in the introduced region (Allen et al., 2016; Meijer et al., 2016; Montti et al., 2016). Hence, some of the differences we observed between projected climate suitability and documented invasion may relate to the extent to which interactions with the local native biota, and other factors not considered here, that can constrain the potential niche.

The use of SDMs can play an important role in assessing regions' vulnerability to particular invasive species, but they also have some limitations that emerging approaches can help to overcome. Importantly, and as discussed already in the context of enemy release, our models were based on abiotic factors only, with no explicit incorporating of biotic factors that determine the potential range of species (Wisz et al., 2013). *Ligustrum lucidum* apparently has high plasticity in ecophysiological traits that allows it to be preadapted to different environmental conditions. One potentially interesting avenue for future work would be to incorporate *L. lucidum* within dynamic models that explicitly represent demographic and dispersal dynamics (e.g. RangeShifter; Bocedi et al., 2014) or that explicitly represent vegetation dynamics (e.g. LPJ-GUESS). Taking such a dynamic approach would potentially capture lags between suitability changes and the species increasing in prevalence through time and across space. A dynamic vegetation model, parameterized to include *L. lucidum*, could be used to assess the degree to which competition with local floral assemblages is likely to influence naturalization and spread dynamics. Furthermore, propagule pressure is not homogeneous. The likelihood of *L. lucidum* naturalizing and spreading can depend strongly upon local land-use and anthropological activities (Gavier-Pizarro et al., 2012; Montti et al., 2017). In particular, *L. lucidum* can be especially likely to become a problematic invasive in regions exhibiting substantial land abandonment. Thus, future work that integrates consideration of climate change and land-use change would be valuable to reveal those regions where climate is likely to become suitable concurrent with land-use change that is likely to favour the establishment of the species. Dynamic coupling of ecological models and land-use models has recently been conducted to explore the interplay between pollination services and land-use (Synes et al., 2018), and there is exciting potential in taking a similar approach for invasive species.

In conclusion, we developed models to predict potential suitable areas for the establishment and spread of *L. lucidum* outside its native area. The main results showed that both current and future potential distribution areas overlap with important hotspots of biodiversity across the world. Threats to hotspots are similar and potentially even more intense than the threats facing biodiversity worldwide. It is important to account for current and potential future spread of invasive plant species into hotspots as they can have massive ecosystem effects, wholly changing hydrology, biogeochemical cycles and, ultimately, biodiversity (Mittermeier et al., 2004). *Ligustrum lucidum* introduction is lead by humans and could invade different hotspots reducing their biodiversity (Fernandez et al., 2020). Hence, these areas should be considered a priority to early detection and control strategies, both under current and future climate change scenarios. Thus, we recommend that the scientific community, policymakers, and stakeholders apply a precautionary principle and design early-warning schemes to detect the emerging invasion risk of *L. lucidum*. Additionally, the implementation of public campaigns about the potential invasive behaviours of this species and local scale strategies can help to prevent the establishment and further spread of *L. lucidum*. Furthermore, global

and regional sharing of information can help to the maintenance of countries alert lists and assist efforts to limit the future invasion of this damaging species.

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CONFLICT OF INTEREST

Authors declare no competing financial or conflict interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Authors have made available codes used for occurrence data cleaning, environmental data processing, and spatial distribution modelling in https://github.com/sjevelazco/Ligustrum_lucidum_modeling

ORCID

Lía Montti https://orcid.org/0000-0003-0301-016X
Santiago José Elías Velazco https://orcid.org/0000-0002-7527-0967
Justin M. J. Travis https://orcid.org/0000-0002-5785-4272
H. Ricardo Grau https://orcid.org/0000-0001-8202-5938

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BIOSKETCHES

The team includes multidisciplinary interests as ecology, conservation and evolutionary aspects of species biology. Their research integrates humans, biodiversity and environment and how these can affect the ecosystem processes simultaneously. They use species distribution model and geographical information systems tools to response question about invasive species, landscape ecology and conservation.

Author contributions: S.J.E.V and L.M contributed equally to this work conceiving the ideas; collecting and processing species occurrence and climate data, constructing species distribution models and analyses. H.R.G and J.T.M.J contributed to discussing ideas, and to writing and editing of the manuscript. All authors –wrote, reviewed and edited the final version.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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