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Fifteen years of monitoring show *Ligustrum lucidum* maintains dominance in invaded forests

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Abstract

1. Invasive tree species alter forest composition and structure of invaded ecosystems. Before implementing management actions for the invasion, it is necessary to understand the dynamics of these species, which requires long-term monitoring. However, most studies on the dynamics of forests dominated by invasive alien species rely on one-time sampling or relatively short monitoring periods.

2. We analyzed the temporal dynamics of forest structure and demography in successional forests dominated by *Ligustrum lucidum*, an invasive alien species in central and northwestern Argentina, over a 15 -year period. We conducted four censuses (2009, 2014, 2019 and 2024) in permanent plots established in *L. lucidum* forests in Sierra de San Javier (Tucumán, Argentina), which were 15, 25, 40 and 60 years old. We assessed changes in tree density, biomass, and mortality and recruitment rates between censuses, both at the plot level and for the four most abundant species (*L. lucidum*, *Morus alba*, *Ocotea porphyria* and *Myrsine laetevirens*).

3. Over the 15-year period, biomass increased significantly in all plots, while tree density declined in two of them. Tree mortality was lower and recruitment was higher during the first intercensal period (2009-2014). At the species level, *M. alba* declined sharply, driven by its high mortality rate. *L. lucidum* persisted as the dominant invasive species, reinforcing its dominance through recruitment and continuous biomass accumulation.

4. Implications**.** This study shows that the replacement of *L. lucidum* by native species during forest succession is unlikely at the temporal and spatial scales considered. Long-term monitoring also revealed that certain native tree species, such as *M. laetevirens* and *O. porphyria*, may be suitable candidates for restoring native forest composition in Yungas forests invaded by *L. lucidum*.

[Keywords: biomass, forest dynamics, tree density, tree mortality, tree recruitment, Yungas]

Resumen. Quince años de monitoreo muestran que *Ligustrum lucidum* sostiene su dominancia en bosques invadidos

1. Las especies arbóreas invasoras alteran la composición y la estructura forestal de los ecosistemas que invaden. Antes de implementar medidas de manejo frente a la invasión, es necesario comprender la dinámica de estas especies; esto requiere monitoreos a largo plazo. La mayoría de los estudios sobre la dinámica de bosques dominados por especies exóticas invasoras se basan en muestreos puntuales o en períodos de monitoreo relativamente breves.

2. Analizamos durante 15 años la dinámica temporal de la estructura y la demografía de bosques sucesionales dominados por *Ligustrum lucidum*, especie exótica invasora en el centro y el noroeste de la Argentina. Realizamos cuatro censos (2009, 2014, 2019 y 2024) en parcelas permanentes en bosques de *L. lucidum* en la Sierra de San Javier (Tucumán, Argentina), con edades de 15, 25, 40 y 60 años. Evaluamos los cambios en la densidad arbórea, la biomasa y las tasas de mortalidad y reclutamiento entre censos, a nivel de parcela y para las cuatro especies más abundantes (*L. lucidum*, *Morus alba*, *Ocotea porphyria* y *Myrsine laetevirens*).

3. La biomasa aumentó en todas las parcelas y la densidad de árboles disminuyó en dos. La mortalidad fue menor y el reclutamiento mayor durante el primer período intercensal (2009-2014). A nivel de especie, *M. alba* mostró un descenso fuerte por su alta mortalidad. *L. lucidum* se mantuvo como especie invasora dominante, conservando esa posición por el reclutamiento y el aumento sostenido de su biomasa.

4. Implicancias. El reemplazo de *L. lucidum* por especies nativas durante la sucesión forestal es poco probable a las escalas temporales y espaciales consideradas. El monitoreo a largo plazo mostró que especies arbóreas nativas como *M. laetevirens* y *O. porphyria* serían buenas candidatas para restaurar la composición nativa de los bosques invadidos por *L. lucidum* en las Yungas.

[Palabras clave: biomasa, dinámica de bosques, densidad arbórea, mortalidad arbórea, reclutamiento arbóreo, Yungas]

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Introduction

The invasion of exotic plant species poses a serious threat to biodiversity conservation, as it is often linked to declines in the local diversity of plants and other organisms (Vitousek et al. 1996; Meiners et al. 2001; Fernández et al. 2020). These species, introduced through human activities, are capable of spreading widely and maintaining ecosystems in an invaded state over long periods (Richardson et al. 2000; Richardson and Rejmánek 2011). Effective management of their spread requires monitoring key parameters (e.g., abundance, biomass, vital rates) to better understand their long-term effects on the dynamics of the ecosystems they invade (Wilson et al. 2014; Marchante et al. 2015; Ceballos et al. 2024).

Plant invasions are dynamic processes that change across time and space, prompting the development of diverse methodologies to study them. Herbarium records have been used to document the expansion of exotic species into new areas (Aikio et al. 2010; Biganzoli et al. 2013), while satellite imagery and aerial photographs have enabled assessments of their spatial spread over time (Visser et al. 2014; Jimenez et al. 2021). Comparisons among sites with different recovery histories or varying times since the last disturbance have also been employed to infer temporal changes in invaded communities (Marco and Paez 2000; Zamora Rivera 2016). Plot-based monitoring has provided insights into temporal variation in community composition, structure and demography, although such studies are often limited to relatively short observation periods (Koop and Horvitz 2005; Kuppinger et al. 2010; Blatnik 2014). While all of these approaches have enhanced our understanding of how invasions change over time, long-term studies remain essential to address key questions. Do invasive species eventually get replaced by other species? Do they persist as dominants? Or do they drive sustained declines in native plant diversity in the long term? (Meiners et al. 2001; Meiners 2007; Marchante et al. 2015).

There is no single dynamic governing invasive alien plants, as they comprise a diverse group of species that colonize a wide range of ecosystems (Richardson and Rejmánek 2011). Although theoretical frameworks describe the invasion process in general terms, once an invasive species becomes established and dominant, invaded communities may follow very different trajectories (Blackburn et al. 2011; Marchante et al. 2015). Consequently, studying their dynamics requires approaches grounded in specific case studies.

As a case study, we focus here on the dynamics of successional forests dominated by *Ligustrum lucidum* W.T. Aiton, an exotic species native to China, originally introduced for ornamental purposes and now invasive in several countries across Asia, Africa, Europe, Oceania and the Americas (Fernández et al. 2020). *L. lucidum* exhibits a strong invasive capacity, attributed to traits such as high germination rates (Montaldo 2000), seed dispersal by numerous bird species, fruit production during periods when other food resources are scarce (Aragón 2000; Montaldo 2000; Panetta 2000), greater survival of seedlings and saplings (Aragón and Groom 2003), faster diameter growth in both juveniles and adults compared with native species (Aragón and Groom 2003; Easdale et al. 2007; Malizia et al. 2017), early sexual maturity (Aguirre-Acosta et al. 2014), high seed and fruit production (Ekert and Bucher 1999; Ferreras et al. 2008), vegetative reproduction (Lichstein et al. 2004), long lifespan (Swarbrick et al. 1999), the ability to recruit both under closed canopies and in open areas (Grau and Aragón 2000), and evergreen foliage that provides a competitive advantage over deciduous species (Montti et al. 2017). Because of these traits, *L. lucidum* competes effectively with native species, leading to local reductions in the diversity of trees (Lichstein et al. 2004), lianas and epiphytes (Ceballos et al. 2015), birds (Ayup et al. 2014), insects (Fernández et al. 2021), amphibians (Guerra et al. 2015) and small mammals (Russo and Jayat 2016). Although these studies have greatly advanced our understanding of the ecological impacts of *L. lucidum*, most are based on single-time surveys or on short-term monitoring, with relatively few addressing its long-term dynamics (Malizia et al. 2017; Ceballos et al. 2024; Malizia et al. 2025).

In the Yungas forests of Argentina, *L. lucidum* dominates invaded stands and is spreading into native successional forests. Over a 20-year period (1991-2011), *L. lucidum* increased its density and basal area in native successional forests from 0.1 to 4%, relating negatively to the growth and survival of neighboring native species (Malizia et al. 2017). In successional forests dominated by *L. lucidum* monitored with permanent plots over a ten-year period (2009-2019), the taxonomic and functional diversity of native trees declined (Ceballos et al. 2024).

Over the same period and in the same plots, biomass in *L. lucidum* forests showed levels comparable to those of mature forests and exceeded those of native successional forests by 56% (Malizia et al. 2025). These previous studies documented how forest structure and diversity changed at the stand level by comparing invaded forests with reference conditions in native forests. Here, we focus on successional forests dominated by *L. lucidum* and extend this work by analyzing stand-level changes over an additional monitoring period (15 years) and by examining the dynamics of individual tree species. We evaluate forest- and species-level structure and demography to determine whether species turnover has occurred within these forests, an aspect that has not been previously examined.

This study contributes to filling a knowledge gap regarding the dynamics of *L. lucidum* in invaded forests, as long-term monitoring of this species in permanent plots remains scarce worldwide (Fernández et al. 2020). The aim of this study was to analyze the temporal dynamics of successional forests dominated by *L. lucidum* over 15 years of monitoring (2009-2024) in Sierra de San Javier (Tucumán, Argentina). We assessed changes in tree density, biomass and mortality and recruitment rates in permanent plots established in *L. lucidum* forests of different ages (i.e., years since land-use abandonment). These changes were also evaluated for the four most abundant species: two invasive species, *L. lucidum* and *M. alba* L., and two native species, *O. porphyria* (Griseb.) van der Werff and *M. laetevirens* (Mez) Arechav. We hypothesize that over the 15-year period, *L. lucidum* has dominated the structure and demography of these forests, due to its high abundance and competitive advantage over native species.

Materials and Methods

Study area

This study was conducted in Sierra de San Javier Park (SSJP), an area of approximately 14000 ha that primarily protects Yungas forests, located in the province of Tucumán, Argentina. The region has a subtropical seasonal climate, with a dry and cool season from April to October (Brown et al. 2001). Average annual precipitation is ~1200 mm, occurring mostly during the summer months (Hunzinger 1997). Mean annual temperature is 18 °C, with summer temperatures that can exceed 35 °C (Hunzinger 1997).

Since the establishment of the SSJP in 1974, the reduction of agricultural and livestock activities has allowed the development of successional forests of different ages (Grau et al. 2010). Part of these successional forests are dominated by native tree species such as *Allophylus edulis (*A. St.-Hil., A. Juss. and Cambess.) Hieron. ex Niederl., *Cedrela angustifolia* DC., *M. laetevirens*, *O. porphyria*, *Blepharocalyx salicifolius* (Kunth) O. Berg., *Pisonia ambigua* Heimerl, *Tecoma stans* (L.) Juss. ex Kunth and *Cupania vernalis* Cambess. (Ceballos et al. 2024; Powell et al. 2025). Other successional forests are dominated by the exotic tree *L. lucidum*, originally introduced for ornamental purposes and primarily established on land previously used for citrus cultivation (Grau and Aragón 2000). Today, *L. lucidum* forests cover around 600 ha in Sierra de San Javier (Montti et al. 2017; Jimenez et al. 2023) and are distributed between 600 and 1450 m a. s. l. (Ayup et al. 2014). In addition to *L. lucidum*, other exotic species such as *M. alba* are present, alongside native Yungas species including *O. porphyria* and *M. laetevirens* (Grau and Aragón 2000). Forests dominated by *L. lucidum* are characterized by a low diversity of native plants both in the understory and the canopy, particulary lianas, epiphytes and trees (Lichstein et al. 2004; Ceballos et al. 2015). The understory is typically impoverished and generally dominated by the native shrub *Psychotria carthagenensis* Jacq., while other species are scarce or absent, suggesting that *L. lucidum* may be limiting their recruitment (Lichstein et al. 2004). In the canopy, tree species diversity is also low, and native trees are generally at a competitive disadvantage compared to *L. lucidum*, as they tend to exhibit lower growth, recruitment and survival rates than this invasive species (Easdale et al. 2007; Powell et al. 2025).

Data collection

For this study, we used data from four permanent plots in successional forests dominated by *L. lucidum*, where this species accounts for 35-97% of the total tree density. These four plots form a chronosequence, representing forests with similar origin or previous land use but differing in forest age, allowing the observation of forest succession 'over time'. This methodology provides an approach to infer temporal changes without waiting decades to observe them directly (Johnson and Miyanishi 2008). Plots were established in forest patches following three criteria: 1) dominance of *L. lucidum*; 2) the same

previous land use, and 3) ages comparable to those of a native successional forest chronosequence already monitored in the area (Zamora Rivera 2016). These plots are part of the Red Subtropical de Parcelas Permanentes (RedSPP), an initiative that monitors Yungas forests in northwestern Argentina since 1991 through periodic vegetation censuses (ier.conicet.gov.ar/red-subtropical-de-parcelas-permanentes-redspp-2). The four *L. lucidum* plots, ranging in size from 0.36 to 1 ha, were established in 2009 on forests that were, previously, citrus orchards with different years since abandonment (Table 1) and have been censused every five years (2014, 2019 and 2024). Each plot is divided into contiguous 20×20 m quadrats. In each census, all trees with a diameter at breast height (DBH at 1.3 m) ≥10 cm were measured at DBH, identified at the species level and permanently tagged with numbered aluminum markers. The same protocol was applied in every census, also recording dead individuals and new recruits that reached the minimum measurement diameter (Osinaga Acosta et al. 2014).

Among the four plots, the 15-year plot showed the highest dominance of *L. lucidum*, whereas in the remaining plots its dominance was relatively lower due to a more mixed tree composition (Table 1). The 15- and 40-year plots were located closer to trails and areas with human presence and showed some signs of anthropogenic disturbance, such as the presence of trash, trees with cut marks and tree stumps. However, these disturbances involved only a few tree individuals and do not appear to have significantly affected forest structure.

Data analyses

Structural variables (tree density and biomass) and demographic variables (mortality and recruitment rates) were calculated within each quadrat. Biomass was estimated using the equation proposed by Chave et al. (2014), which incorporates DBH, height and wood density, considering all tree stems with DBH>10 cm. Tree height for the different species recorded in the quadrats was estimated using the Michaelis-Menten function (Equation 1).

$$\text{Height} = (A \times \text{DBH}) / (B + \text{DBH}) \qquad \text{Equation 1}$$

where A and B are parameters specific to montane forests (Blundo et al. 2025). Specifically for *L. lucidum*, a model with species-specific A and B parameters was generated using the BIOMASS library (Réjou-Méchain et al. 2017). Wood density values were obtained from local sources (INTI-CITEMA 2003; Easdale et al. 2007). For species not included in these sources, values were obtained from the global database of Chave et al. (2006). The annual mortality rate was calculated with Equation 2.

$$ma = 1 - (NsT / N_0)^{1/T} \qquad \text{Equation 2}$$

where N_0 is the number of individuals recorded in the previous census; NsT is the number of survivors in the subsequent census, and T is the interval between censuses (Kohyama et al. 2018).

The annual recruitment rate was calculated with Equation 3.

$$ra = 1 - (NsT / NT)^{1/T} \qquad \text{Equation 3}$$

where NsT is the number of survivors and NT the total number of individuals recorded in the subsequent census (Kohyama et al. 2018).

We then analyzed changes in structural and demographic variables between censuses using generalized linear models (GLM) and

Table 1. General data of permanent plots established in successional forests invaded and dominated by *L. lucidum* in Sierra de San Javier (Tucumán, Argentina). Forest age was measured as years since land-use abandonment. *L. lucidum* dominance (%) represents the proportion of individuals of this species relative to the total number of trees recorded in each plot.

Tabla 1. Información general de las parcelas permanentes establecidas en bosques sucesionales invadidos y dominados por *L. lucidum* en la Sierra de San Javier (Tucumán, Argentina). La edad del bosque se calculó como los años desde el abandono del uso del suelo. La dominancia de *L. lucidum* (%) representa la proporción de individuos de esta especie relativo al número total de árboles registrados en cada parcela.

Plot	Forest age (years)	Area (ha)	Elevation (m a. s. l.)	Number of 20x20 m quadrats	*L. lucidum* dominance (%)	Number of *L. lucidum* individuals in 2024
LIG15	15	0.64	645	16	97	506
LIG25	25-30	1	732	25	35	125
LIG40	40-45	1	619	25	58	134
LIG60	60	0.36	659	9	60	92

mixed-effects generalized linear models (GLMM) in R (R Core Team 2025). Structural variables represent the state of the forest at the time of each census (i.e., density and biomass), and therefore the census year was treated as a continuous variable. In contrast, intercensal periods (i.e., 2009-2014, 2014-2019, 2019-2024) were treated as categorical for demographic variables because they reflect processes occurring between censuses, such as tree recruitment and mortality.

We fitted four candidate models of increasing complexity: a GLM assuming independent observations (model 1), a GLMM with random intercepts for quadrats nested within plots (model 2), a GLMM including plot × census interactions, assuming plot-specific temporal trajectories (model 3), and a GLMM including plot x census interactions and quadrat coordinates (x, y) as fixed effects (model 4). Model 1 served as a baseline assuming independent observations, against which the remaining models were compared. Model 2 addressed the hierarchical structure of the data (quadrats as pseudoreplicates nested within plots) by incorporating random intercepts for quadrats, thereby accounting for the non-independence among observations within the same plot. Model 3 extended this by allowing plot-specific temporal trajectories through a plot × census interaction, recognizing that forests of different ages may follow distinct successional pathways. Finally, Model 4 accounted for potential spatial gradients within plots by including quadrat coordinates as fixed effects, capturing fine-scale variation in forest structure that may not be explained by successional age alone.

GLM were fitted using the stats package in R (R Core Team 2025), and GLMM were fitted using the nlme package (Pinheiro et al. 2023). Models were estimated using maximum likelihood (ML) to allow comparison among models with different fixed-effect structures. Gaussian error distributions were used for all response variables, as model residuals showed no strong deviations from normality or major skewness. No transformations were applied to the data. Model results were interpreted based on the β coefficients, which represent the magnitude of change in the response variables; for example, for tree density the coefficients indicate the change in the number of individuals per quadrat per year.

For each structural and demographic variable, we compared models using Akaike's Information Criterion (AIC) and selected the model providing the best trade-off between explanatory power and parsimony (Supplementary Material-Table S1).

To evaluate changes in *L. lucidum* at the species level, we applied the same model structure used in the community-level analysis, fitting four models to evaluate tree density, biomass, mortality and recruitment, and then selecting the best model using AIC. For *M. alba*, *M. laetevirens* and *O. porphyria*, we only described temporal changes without conducting statistical analyses, as these species occurred in only a few quadrats, which limited the number of pseudoreplicates available for analysis.

Results

For tree density and biomass, the best-fitting model included the interaction between plot and census, which allowed each plot to have its own temporal trajectory (model 3). The results of the model showed that tree density did not show a uniform pattern across plots. Tree density declined in all plots, but the decrease was statistically significant only in LIG25 and LIG60 (Figure 1A, Table 2). The estimated decrease was approximately 0.30 and 0.17 individuals.quadrat^{-1}.year^{-1} in LIG25

Table 2. Changes in tree density and biomass between 2009 and 2024 in *L. lucidum* quadrats monitored in the Sierra de San Javier, Tucumán, Argentina. Each row in the table represents the interaction between forest plot and census year.

Tabla 2. Cambios en la densidad y biomasa arbórea entre 2009 y 2024 en cuadrantes de *L. lucidum* monitoreados en la Sierra de San Javier, Tucumán, Argentina. Cada fila en la tabla representa la interacción entre la parcela de bosque y el año del censo.

Response variable	Explanatory variable	β	Standard error	DF	t	P
Tree density	Census:LIG15	-0.0413	0.03223	221	-1.280	0.2019
	Census:LIG25	-0.3028	0.04127	221	-7.335	<0.0001
	Census:LIG40	-0.0396	0.04127	221	-0.958	0.3390
	Census:LIG60	-0.1654	0.05371	221	-3.080	0.0023
Tree biomass	Census:LIG15	0.1900	0.02098	221	9.059	<0.0001
	Census:LIG25	0.0843	0.01853	221	4.549	<0.0001
	Census:LIG40	0.0572	0.01310	221	4.364	<0.0001
	Census:LIG60	0.0729	0.02547	221	2.861	0.0046

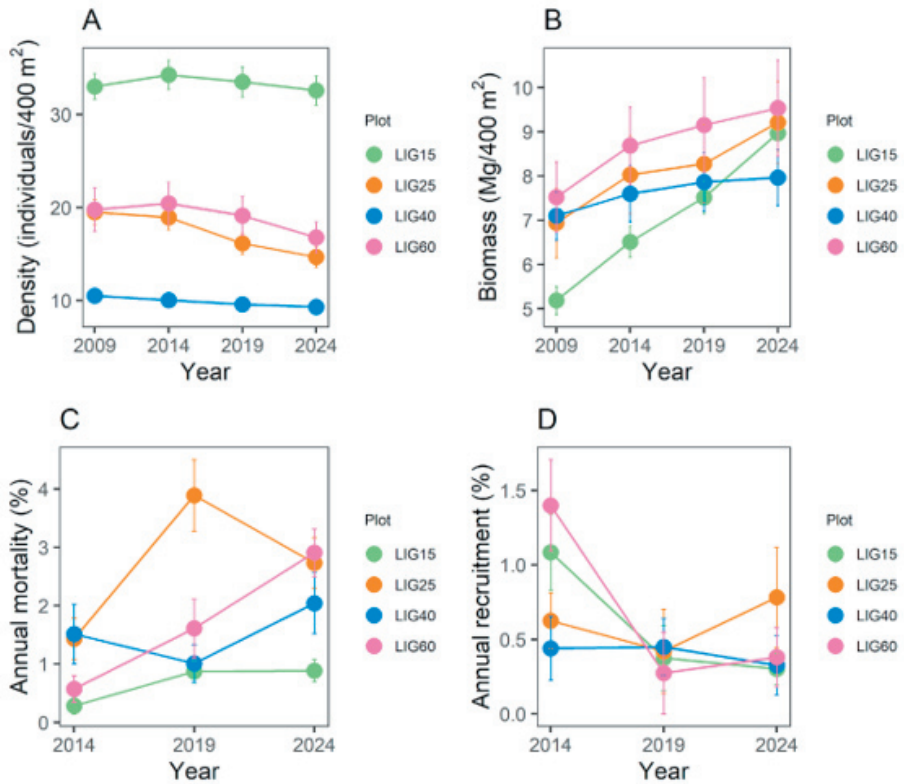

Figure 1. Changes in tree density (A), biomass (B), mortality (C), and recruitment (D) for trees in four *L. lucidum* forest plots, across four censuses conducted in 2009, 2014, 2019 and 2024 in the Sierra de San Javier, Tucumán, Argentina. Means for quadrats within each plot are shown with their respective standard errors. In figures C and D, the census year corresponds to the final year of the intercensal period over which the variables were calculated.

Figura 1. Cambios en la densidad arbórea (A). biomasa (B), mortalidad (C) y reclutamiento (D) en cuatro parcelas de bosque de *L. lucidum*, a través de cuatro censos realizados en 2009, 2014, 2019 y 2024 en la Sierra de San Javier, Tucumán, Argentina. Los promedios de los cuadrantes dentro de cada parcela se muestran con sus errores estándar correspondientes. En las figuras C y D, el año del censo corresponde al año final del período intercensal en el que se calcularon las variables.

and LIG60, respectively. In other words, each quadrat lost an average of 3 to 5 trees over a 15-year period in LIG60 and LIG25, respectively. In contrast, tree biomass increased significantly in all plots between 2009 and 2024, although the magnitude of the increase differed among them (Figure 1B, Table 2).

Regarding vital rates, annual mortality was modeled using the same interaction model applied for structure variables, capturing plot-specific temporal trajectories (model 3). In contrast, recruitment rate was best described by a random-intercept model without interaction (model 2). Annual mortality rate was significantly lower during the first intercensal period (2009-2014) compared to 2014-2019 and 2019-2024 (Figure 1C, Table 3). Conversely, recruitment rate was significantly higher in 2009-2014 relative to the subsequent periods (Figure 1D, Table 3). Mortality was higher in plots LIG25 and LIG60, whereas recruitment rates remained relatively similar across plots. On average, mortality ranged from 1 to 2% per year, exceeding recruitment, which ranged from 0.5 to 1% per year (Figure 1C-D).

To describe changes between censuses in the density and biomass of *L. lucidum*, the best-ranked models included the interaction between census and plot (Supplementary Material-Table S2). Tree density increased significantly in LIG15, whereas biomass increased significantly in plots LIG15 and LIG25 (Supplementary Material-Table S3). Although biomass increased for *L. lucidum* in all plots, it nearly doubled in quadrats within these two plots, from 4.98 to 8.79 Mg in LIG15 and from 2.85 to 4.63 Mg in LIG25 between the first and the last census. For mortality and recruitment rates of *L. lucidum*, the best-ranked model was Model 2 without interaction. Mortality rate increased significantly between the first and the last intercensal period, whereas recruitment rate

Table 3. Comparisons of mortality and recruitment rates among intercensal periods in *L. lucidum* forest quadrats in the Sierra de San Javier, Tucumán, Argentina.

Tabla 3. Comparaciones de las tasas de mortalidad y reclutamiento entre períodos intercensales en cuadrantes de bosque de *L. lucidum* en la Sierra de San Javier, Tucumán, Argentina.

Variable	Comparison between intercensal periods	Estimation	Standard error	DF	*P*
Tree mortality rate	(2009-2014) vs. (2014-2019)	-0.895	0.355	142	0.0340
	(2009-2014) vs. (2019-2024)	-1.190	0.355	142	0.0029
	(2014-2019) vs. (2019-2024)	-0.296	0.355	142	0.6833
Tree recruitment rate	(2009-2014) vs. (2014-2019)	0.5065	0.166	142	0.0076
	(2009-2014) vs. (2019-2024)	0.4389	0.166	142	0.0245
	(2014-2019) vs. (2019-2024)	-0.0676	0.166	142	0.9127

was significantly higher in the first intercensal period and then decreased (Figure 2C-D, Supplementary Material-Table S4).

Between 2009 and 2024, the density of *M. alba* declined, whereas the densities of *O. porphyria* and *M. laetevirens* remained relatively stable (Figure 2A). Over the same period, the biomass of *M. alba* decreased and that of *O. porphyria* increased, whereas the biomass of *M. laetevirens* remained relatively constant (Figure 2B). Mortality was particularly high for *M. alba*, whereas recruitment was low for all species except *L. lucidum* (Figure 2C-D).

Discussion

This study described the temporal dynamics of successional forests dominated by *L. lucidum* in the Yungas of Tucumán, and its structural and demographic changes over a 15-year period. We analyzed these changes in four permanent plots ranging from 15 to 60 years since forest establishment on abandoned

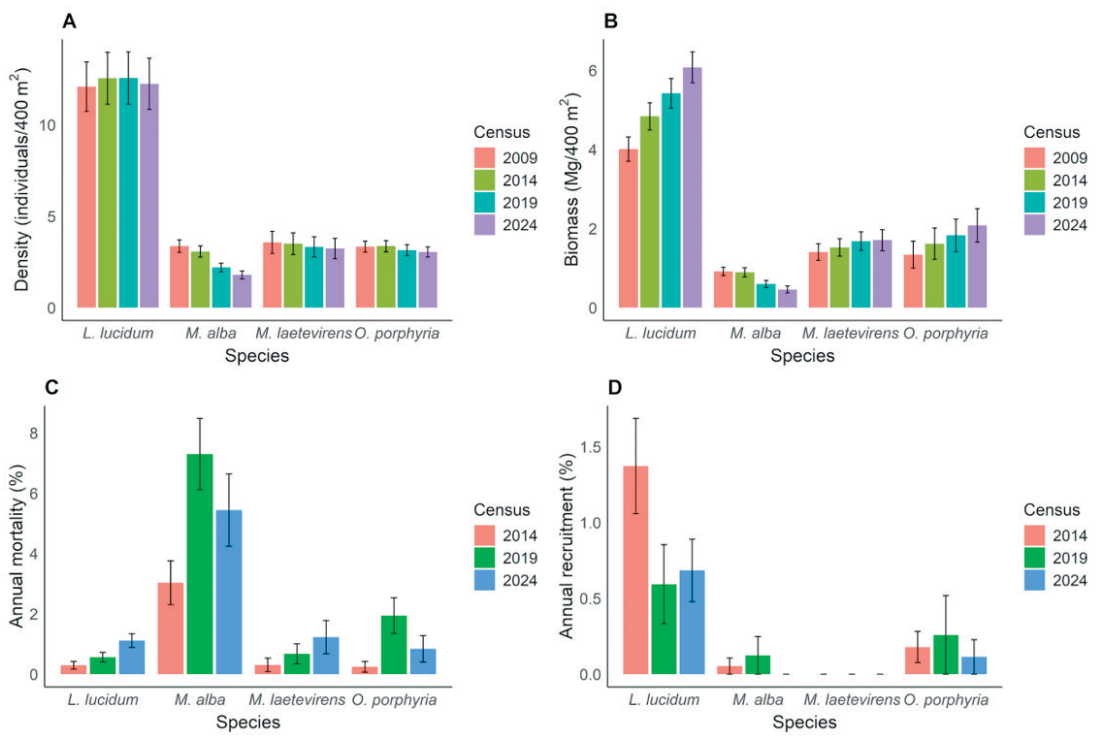

Figure 2. Changes in tree density (A), biomass (B), mortality (C), and recruitment (D) for trees for the four most abundant species (*L. lucidum*, *M. alba*, *M. laetevirens* and *O. porphyria*) in *L. lucidum* forests in the Sierra de San Javier, Tucumán, Argentina. Bars represent the mean value of each variable for each species in each census, considering only the quadrats in which they were present, with their respective standard errors. In figures C and D, the census year corresponds to the final year of the intercensal period over which the variables were calculated.

Figura 2. Cambios en la densidad arbórea (A). biomasa (B), mortalidad (C) y reclutamiento (D) para las cuatro especies más abundantes (*L. lucidum*, *M. alba*, *M. laetevirens* y *O. porphyria*) en bosques de *L. lucidum* en la Sierra de San Javier, Tucumán, Argentina. Las barras representan el promedio de la variable para cada especie en cada censo, considerando solamente los cuadrantes en los que estaban presentes, con sus respectivos errores estándar. En las figuras C y D, el año del censo corresponde al año final del período intercensal en el que se calcularon las variables.

citrus orchards, an age range that is relevant to the life cycle of this species (i.e., *L. lucidum* can reach sexual maturity in less than 10 years and live for 50-100 years) (Swarbrick et al. 1999; Aguirre-Acosta et al. 2014). Within the time span considered here, the invasive species was not replaced by others in any of the plots, possibly due to its longevity and clonal reproduction, which allow individuals to persist for many years (Fernández et al. 2020).

During the 15 years of monitoring, individual density tended to decrease in all plots, particularly in two of them. This trend may be explained by mortality rates exceeding recruitment rates. In contrast, biomass increased in all plots, possibly because biomass growth of surviving trees compensated for biomass losses due to mortality. In none of the plots was *L. lucidum* replaced by other species, likely due to its high initial density and its combination of pioneer and shade-tolerant traits (Fernández et al. 2020). For instance, it combines early establishment, rapid diameter and height growth and high seed production —characteristics typical of pioneer species— with high wood density and shade tolerance, attributes more typical of dominant species in later successional stages (Fernández et al. 2020).

The most notable demographic change in the plots was the decline in the density of *M. alba*, the second most dominant tree species after *L. lucidum*. This reduction was primarily driven by its high mortality rate, which ranged from 3% to 8% per year. This pattern was expected, as *M. alba* establishes under high-light conditions but has low shade tolerance. Consequently, as succession advances, it is outcompeted by taller species —mainly *L. lucidum*—, which reduce its chances of survival (Grau and Aragón 2000). A previous study in these plots showed that *M. alba* tends to decline with forest age, suggesting that its density would decrease as forests mature (Zamora Rivera 2016). The present study confirms this trend by documenting a continuous reduction of the species over 15 years of monitoring in permanent plots.

Although this study did not focus on understory regeneration, previous studies conducted in these same plots more than 15-20 years ago (Lichstein et al. 2004; Bartolucci 2011) provide context to assess whether the seedlings and saplings recorded then later became part of the adult tree layer or increased in abundance. These studies showed that the dominance of *L. lucidum* does not limit the initial recruitment of native species, although a negative effect was detected in larger sapling size classes, possibly due to mortality (Lichstein et al. 2004). Likewise, no differences were found in the richness or abundance of saplings under *L. lucidum* trees compared with native trees (Bartolucci 2011). The most abundant species in the regeneration included *B. salicifolius*, *L. lucidum*, *C. vernalis*, *A. edulis*, *O. porphyria* and *M. laetevirens* (Bartolucci 2011). Currently, only the latter two native species are among the most abundant in the plots after *L. lucidum*, whereas the others are present but at low abundance. The causes of this pattern are unclear and may be related to sapling mortality or lower growth rates, highlighting the importance of continued monitoring to determine whether these species will become more abundant and a more important component of the canopy in the future.

The patterns observed in this study provide technical information for potential management and restoration of native species in forests invaded by *L. lucidum*. Numerous studies have documented the impacts of this exotic species on native biodiversity, affecting both the floristic and faunal composition of invaded forests (Lichstein et al. 2004; Ayup et al. 2014; Ceballos et al. 2015; Guerra et al. 2015; Russo and Jayat 2016; Fernández et al. 2021). In response, management actions focused on reducing its impact have been implemented in the Yungas, including the removal of *L. lucidum* individuals and the planting of native tree seedlings (Lambin et al. 2020). Passive restoration (i.e., natural regeneration without active management) may not be the most effective strategy, as the species maintained its dominance and increased its biomass over 15 years of monitoring. However, this inference should be interpreted cautiously, as longer-term monitoring and greater plot replication are required to confirm this pattern.

Long-term monitoring also showed that certain native species, such as *M. laetevirens* and *O. porphyria*, maintained or even increased their biomass during the study period. Previous studies have noted that both share demographic traits with *L. lucidum* —such as relatively high growth and survival rates (Powell et al. 2025)—, suggesting that they could be effectively incorporated into active restoration strategies. In addition, both species are shade-tolerant and have been recorded

as established saplings beneath *L. lucidum* canopies (Bartolucci 2011), indicating their ability to recruit and grow under the low-light conditions typical of these forests. They also reach heights similar to or even exceeding those of *L. lucidum* (~24-29 m) (Easdale et al. 2007), which may allow them to reach the canopy. Both species may therefore be good candidates for ecosystem restoration because they play important ecological roles: they are shade-tolerant canopy species that produce fleshy fruits consumed and dispersed by birds, and *O. porphyria* in particular is a key host species for epiphytes in the Yungas (Easdale et al. 2007; Ceballos 2022).

A limitation of this study is the use of a chronosequence design with a single plot per successional age, which precludes the full statistical separation of age-related effects from site-specific characteristics such as topography, soil properties, or local disturbance history. Previous studies have examined how different environmental, landscape, and land-use history variables influence the spatial distribution of *L. lucidum* (Aragón and Morales 2003; Montti et al. 2017); however, how these factors affect its temporal dynamics remains insufficiently understood.

Conclusions

This study revealed that successional forests dominated by *L. lucidum* monitored for 15 years in four permanent plots in Sierra de San Javier Park (Tucumán, Argentina) exhibit a long-term arrested successional stage, characterized by the sustained dominance of this invasive species and the absence of replacement by native or other tree species. Despite increases in biomass across all plots, *L. lucidum* remained the structurally and demographically dominant species, suggesting a self-reinforcing invasion dynamic that maintains forest structure over time. The decline of *M. alba*, linked to its low shade tolerance, further reinforces the competitive advantage of *L. lucidum* in invaded stands.

These findings demonstrate that, under natural conditions and in the absence of significant disturbances, *L. lucidum* can sustain its invasion for decades in these forest plots, making its eradication or natural replacement by native species highly unlikely. However, the observed persistence and biomass of certain native species (e.g., *M. laetevirens* and *O. porphyria*) highlight their potential role in active restoration strategies aimed at gradually reintroducing native diversity into invaded stands.

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