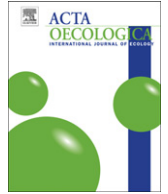


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Original article

Exotic species as modifiers of ecosystem processes: Litter decomposition in native and invaded secondary forests of NW Argentina

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ABSTRACT

Invasions of exotic tree species can cause profound changes in community composition and structure, and may even cause legacy effect on nutrient cycling via litter production. In this study, we compared leaf litter decomposition of two invasive exotic trees (*Ligustrum lucidum* and *Morus* sp.) and two dominant native trees (*Cinnamomum porphyria* and *Cupania vernalis*) in native and invaded (*Ligustrum*-dominated) forest stands in NW Argentina. We measured leaf attributes and environmental characteristics in invaded and native stands to isolate the effects of litter quality and habitat characteristics. Species differed in their decomposition rates and, as predicted by the different species colonization status (pioneer vs. late successional), exotic species decayed more rapidly than native ones. Invasion by *L. lucidum* modified environmental attributes by reducing soil humidity. Decomposition constants (*k*) tended to be slightly lower (–5%) for all species in invaded stands. High SLA, low tensile strength, and low C:N of *Morus* sp. distinguish this species from the native ones and explain its higher decomposition rate. Contrary to our expectations, *L. lucidum* leaf attributes were similar to those of native species. Decomposition rates also differed between the two exotic species (35% higher in *Morus* sp.), presumably due to leaf attributes and colonization status. Given the high decomposition rate of *L. lucidum* litter (more than 6 times that of natives) we expect an acceleration of nutrient circulation at ecosystem level in *Ligustrum*-dominated stands. This may occur in spite of the modified environmental conditions that are associated with *L. lucidum* invasion.

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1. Introduction

The introduction of an exotic plant species in a new environment may alter species composition (e.g., changing richness and relative abundance of native species), environmental characteristics (e.g., light and water availability), and species interactions (e.g. dispersal and herbivory). These changes may affect the different controls of litter decomposition rates (Meentemeyer, 1978; Melillo et al., 1982; Couteaux et al., 1995; Cornelissen, 1996; Wardle and Lavelle, 1997; Parton et al., 2007; Cornwell et al., 2008) by modifying the timing, abundance and quality of the litter inputs (Vitousek and Walker, 1989; Dascano et al., 1994; Evans et al., 2001), or the physical properties of the environment (Mack and D'Antonio, 2003; Siemann and Rogers, 2003; Ashton et al., 2005;

Hobbie et al., 2006). These effects may, in turn, influence the abundance, identity and activity rates of soil biota (Ehrenfeld, 2003; Wolfe and Klironomos, 2005). Consequently, nutrient cycling at ecosystem scale may be slowed down or speeded up by exotic invasions (Liao et al., 2008; Godoy et al., 2010).

Woody species are amongst the most successful plant invaders (Cronk and Fuller, 1995) and they often show characteristics of pioneer or early successional species (Baruch and Goldstein, 1999; Funk and Vitousek, 2007). They have high growth rate and plasticity, elevated specific leaf area, lower leaf construction cost, colonize early during the succession establishing in disturbed habitats (edges or abandoned fields), are shade-intolerant, and have short life span (Baruch et al., 1985; Bazzaz, 1986; Pattison et al., 1998; Baruch and Goldstein, 1999; Allison and Vitousek, 2004; Lake and Leishman, 2004; van Kleunen et al., 2009; Tecco et al., 2010). However, invasive species display a broad range of attributes and colonization strategies. For example, successful invaders in forested landscapes may combine early successional characteristics (high

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seed production, fast growth rate) with late successional ones (shade-tolerance, high competitive ability) (Cronk and Fuller, 1995; Martin et al., 2010). These different life history characteristics are often associated to a broad range of leaf attributes. Consequently, exotic species effects on litter decomposition may strongly depend on its life-history traits.

In this work, we evaluated the decomposition rates of leaf litter from two exotic tree species – *Morus* sp. (Moraceae) and *Ligustrum lucidum* (Oleaceae) – and two of most abundant native trees – *Cinnamomum porphyria* (Lauraceae) and *Cupania vernalis* (Sapindaceae) – in invaded and native secondary mountain forest stands of NW Argentina. We explored the effect of invasive exotic species on litter decomposition via changes in litter quality and environmental characteristics by measuring leaf attributes and comparing decomposition rates in invaded (*Ligustrum*-dominated) and native forest stands. We predicted that *Morus* sp. (a pioneer species) will have the highest decomposition rate, while *L. lucidum* (a late pioneer) will show a decomposition rate similar to native, old successional species. In addition, we expect lower decomposition rates in *Ligustrum* than in native stands since stands invaded by *L. lucidum* show higher canopy cover than native ones and are less diverse in terms of tree species (Lichstein et al., 2004), litter types (Ayup et al., this issue) and, potentially, in soil biota. However, the environmental characteristics of modified habitats might interact with exotic litter characteristics affecting the final outcome.

2. Methods

2.1. Study site

The study was conducted in the lower mountain forest of Sierra de San Javier, Tucumán, Argentina (26° 70' S, 65° 35' W) at approximately 800 m.a.s.l. The study sites are located within a protected area that belongs to the University of Tucumán (Fig. 1).

The area represents the southernmost limit of subtropical Andean mountain forest (also known as *Yungas*) which extends from Bolivia to Catamarca province in Argentina (Cabrera and Willink, 1980; Grau and Brown, 1995). Average annual precipitation ranges from 1300 to 1500 mm distributed in a monsoonal regime with dry winters and rainy summers (Bianchi and Yañez, 1992). During the winter water supplies result mainly from horizontal rain (Hunzinger, 1995). Mean annual temperature is 18 °C with frosts occurring from June to August. The vegetation corresponds to semideciduous mountain forest with three strata: a canopy is approximately 30 m tall (dominated by *Blepharocalyx salicifolius* and *Cinnamomum porphyrium*), a subcanopy is 12–15 m tall dominated by *Piper tucumanun*, *Eugenia uniflora* and *Allophylus edulis*, and an understory with shrubs approximately 3 m tall (mainly dominated by *Psychotria cartagenensis*) (Malizia et al., 2010). Yungas forest constitutes one of the most diverse biomes in Argentina (Brown, 1995).

Most of Sierra de San Javier piedmont was cleared for crop production and grazing during the early twentieth century (Brown et al., 2001), but in the last two decades many cleared areas were abandoned and currently show different forest regeneration stages (Grau and Aide, 2007; Grau et al., 2008). The composition of these secondary forest stands depends on previous land use and time since abandonment (Grau et al., 1997). Importantly, many of these stands are colonized by several exotic species, but *L. lucidum* is the only invasive species that forms monodominant forest stands in this area. *Ligustrum*-dominated stands show lower diversity of trees, shrubs and lianas (Aragón and Morales, 2003; Lichstein et al., 2004), a simplified vertical structure, higher biomass (associated to its high growth rate), canopy cover (Easdale et al., 2007; Lichstein et al., 2004), and density (more than 500 ind./ha) (Grau et al., in press). Invaded stands also show a thinner litter layer than native forest stands of the same age (Ayup et al., this issue). Even though *Morus* sp. is very abundant in many forest stands, it does not reach

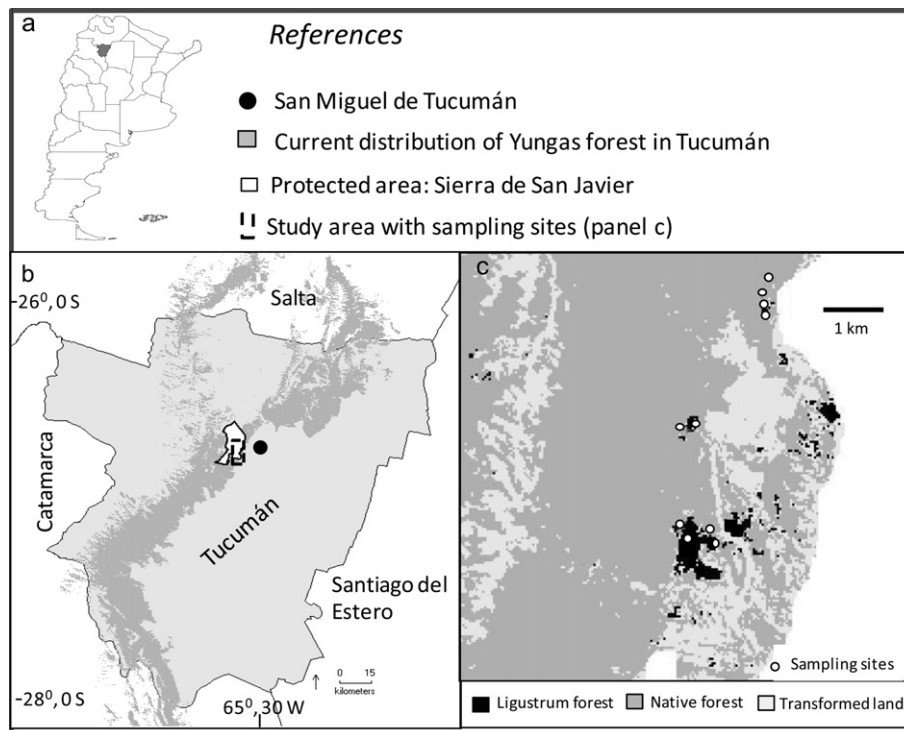


Fig. 1. (a) Tucumán province, (b) location of the Study Area in Tucumán, and (c) SW of Sierra de San Javier protected area where the sampling sites were located. Different colors indicate different land cover (forest types) described by a remote sensing classification.

the canopy and it shares its dominance with other exotic (such as *Ligustrum*) and native species. For this reason, this study only compares stands invaded by *Ligustrum* with native forest ones.

2.2. Studied species

Ligustrum lucidum is an Asian tree that colonizes areas with different land-use history and age. Although it is more abundant in secondary forest stands, it also grows in gaps in old-growth forests (Aragón and Morales, 2003). Its seeds germinate and its seedlings survive in multiple locations such as edges, gaps, and also in shaded forest understory (Aragón and Groom, 2003). For this reason, Easdale et al. (2007) assigned an intermediate value in the pioneer index to this species. This index goes from 1 to 3 according to the species recruitment capacity under different light conditions (i.e., 1: the species recruits only under canopy shade, 2: the species recruits in different cover situations, and 3: the species recruits only in open places under full-light conditions). This is an evergreen, shade-tolerant and rather long-lived species with relatively hard wood and high resprout capacity (Aragón and Groom, 2003; Lichstein et al., 2004). This species reaches the canopy strata (Aragón and Morales, 2003; Easdale et al., 2007), and its stands have a very close canopy and dark understory (Lichstein et al., 2004; Ayup et al. this issue). Due to its characteristics *L. lucidum* has been placed in the conservative resource acquisition extreme in the exotic trait spectrum in a study that screened almost 40 exotic species of central Argentina (Tecco et al., 2010). Importantly, its distribution is expected to expand in the near future (Grau et al., 2008).

Like *L. lucidum*, *Morus* sp. is also of Asian origin, but it is a deciduous species that is surpassed in height by native canopy trees during succession (maximum height 17 m) (Grau et al., 1997; Easdale et al., 2007). It is abundant in secondary forest stands that were originally abandoned citrus crops, and it is more prevalent in edges and open areas. As it is more abundant in edges, and frequently dies out in patches older than 50 years, it appears to be shade intolerant. It is considered a pioneer species (pioneer index = 3, Easdale et al., 2007). Although we do not have enough information about its functional attributes, it is likely part of the rapid resource acquisition extreme (Peñuelas et al., 2010).

The native species included in this study are the most abundant in the canopy (*C. porphyria*) or in the subcanopy and as saplings (*Cupania vernalis*). Both are late successional, bird dispersed, and with a high growth rate in relation to the rest of native species in the area (Easdale et al., 2007). *C. porphyrium* is a semi-deciduous, tall (29 m maximum height), shade tolerant, late successional species. It is very abundant in canopy stratum in secondary (more than 25 years old) and old growth forests (Grau et al., 1997; Easdale et al., 2007). *C. vernalis* has similar life history characteristics, but smaller height (22 m maximum height), and it rarely reaches the canopy. *C. vernalis* saplings account for approximately 70% of the saplings in native and invaded forest understory (Grau et al., 1997; Lichstein et al., 2004). Easdale et al. (2007) listed *C. porphyria* and *C. vernalis* as recruiters only under canopy shade (pioneer index = 1). Interestingly, five-year data from permanent plots indicated that *Morus* sp. and *C. porphyria* have similar maximum growth rate, while *C. vernalis* grows slower. *L. lucidum*'s maximum growth rate was found to be more than twice as much as that of the other species (Easdale et al., 2007).

2.3. Data collection and experimental design

To isolate the effect of exotic species on litter quality and environmental modifications, we set up a litter incubation experiment in two types of forest: stands invaded by *L. lucidum* (with a *L. lucidum* density >500 ind./ha; hereafter *Ligustrum* forest), and

native stands. We used a paired design with 5 stands for each forest category (5 *Ligustrum*–Native forest pairs). In all cases, forest stands were similar in age (between 30 and 50 years of succession), altitude, slope and soil type, and were larger than 2 ha. Pairs were determined by the closest similarity in terms of age and previous land-use, and spatial proximity. We collected freshly senesced leaves of all species from May to September 2010 using cotton fabric pieces suspended above the soil as leaf traps. Leaves were air-dried from three to five days and stored in open paper bags until further analysis. We prepared litter bags (20 × 20 cm, 2 mm fiberglass mesh) with 2 g of leaf litter from each species. They were then placed in 2 × 2 m permanent plots in each of the 5 forest stands per forest type from where the superficial detritus had been removed. Litterbags were placed in the field in September 2010 (4 litterbags × 4 species × 2 forest types × 5 replicates = 160 litterbags), and harvested 50, 123, 269 and 365 days later. At each harvest, the remaining material was carefully brushed, dried at 60 °C for 3 days, and weighed. We measured ash content (ignition at 600 °C) in a subset of samples to correct for sand or clay contamination.

Before beginning with the experiment we measured three physical and two chemical leaf attributes. Litter water content was calculated as the percentage of water in senesced and dried leaves (60 °C for three days), while specific leaf area (SLA) was computed as the ratio of the leaf surface to its dried weight (mm²/g). Leaves were scanned (as soon as they were collected) and leaf surface was measured using Scion Image Software (National Institute of Health, Bethesda, MD, USA). Tensile strength or leaf toughness (in Newtons/mm) was measured as an index of litter physical quality (Vivanco and Austin, 2006; Tecco et al., 2010) in 5 leaves from each species. Litter water content, SLA and leaf toughness were measured on recent senescent leaves with no signs of shrinking because of desiccation or herbivore damages. Litter chemical composition (%C, %N and C:N) was assessed as an indication of litter quality. Total C and N contents were determined by dry combustion with Carlo-Erba NA 2500 elemental analyser at IFEVA, Facultad de Agronomía, Universidad de Buenos Aires. In addition, two environmental variables were considered: soil temperature (10 measurements per replicate with *Optris*, *Minisight* infrared radiometer) and soil relative humidity (with 3 soil cores taken at 5–10 cm deep in each replicate). Both variables were measured every harvest day. Soil samples were oven-dried at 105 °C for 48 h and gravimetric soil water content was calculated as the difference between wet and dry weights. Data on canopy cover percentage from the same sites was available from a related study (Ayup et al. this issue).

2.4. Data analysis

To describe litter decay dynamics in the four species we compared linear, single exponential, and hyperbolic models using maximum likelihood. To compare the relative fit of the models we used Akaike information criteria (Bolker, 2008). We also used Akaike criteria to evaluate if a more complex model considering different rates for the distinct forest types for each species was more suitable. We later used the model that presented the best fit to analyze the differences among species and forest types. We used a single exponential model of the form:

$$y = a \cdot \exp^{-kt}$$

where y corresponds to the percent of remaining litter weight at time t , a is the initial percent litter weight, and k is the decomposition rate. When this equation is expressed in logarithms, k becomes the slope of a linear relationship, and is commonly known as the decomposition constant (Swift et al., 1979). Computing k in this

way allowed us to compare our results with those of other studies that considered different species and ecosystems. We later compared k values among species and forest types using a two-way ANOVA with species, forest types and their interaction as sources of variation. In addition, we calculated the time required for 50% ($T_{50} = 0.693/k$) and 95% ($T_{95} = 3/k$) decay of the original litter mass (Singh and Singh, 1999).

We used a repeated measures ANOVA to test for differences in soil temperature and humidity in different forest types throughout the study period. We used a one-way ANOVA to test for differences in leaf chemical (%N, %C and C/N) and physical characteristics (tensile strength, litter water content and SLA) between litter types. In the case of percent litter water content, we used Kruskal–Wallis non-parametric test due to lack of normality. Data were analyzed using basic and *bbmle* (tools for general Maximum Likelihood estimation) packages of R program (R Development Core Team, 2010).

3. Results

3.1. Litter decomposition rate: differences among species and forest types

Decomposition curves were similar in all species and they could be appropriately described by a negative exponential function (Fig. 2). This model showed a better fit than linear or hyperbolic functions ($\Delta AIC > 5$) in all cases. However, even though in general

the curves were similar, there was a clear difference among species. The exotics showed a more marked decay, especially early in the experiment (50 and 123 days), while native species decay was slower and closer to linear. More than 50% of the litter of native species remained in the bags after a year of incubation. *C. porphyria* and *C. vernalis* decomposition rates were between 6 and 12 times lower than those of exotic species. Notably, there was also a difference between exotic species with *L. lucidum* decomposing almost 35% slower than *Morus* sp. By the third sampling date (123 days) the percentage of litter remaining was about 20% in *Morus* sp. litterbags, 35% in *L. lucidum*, and 70% in *C. porphyria* and *C. vernalis*.

Decomposition constants (k) were significantly different among species ($F_{3,28}$ for species = 136.28, $p < 0.001$). *Morus* sp. showed the highest decay rate over time and it significantly differed from those of the rest of the species (Fig. 3). *Morus* sp. decomposition constant was followed by that of *L. lucidum*, while there was no difference between the two natives. About 50% of leaf weight (T_{50} or litter half-life) was lost in approximately two months in the case of *Morus* sp., and three months in the case of *L. lucidum*. *C. porphyria* and *C. vernalis* litter half-lives were more than a year (Table 1). Ninety five percent of *Morus* sp. and *L. lucidum* leaf litter (T_{95}) is expected to be decomposed in six and 12 months, respectively, while T_{95} of natives was about 5 years.

Decomposition constants showed slightly lower values in *Ligustrum* forests (Fig. 3) than in native forest stands for all species, except for *C. vernalis* ($F_{1,28}$ for forest types = 4.45, $p = 0.045$).

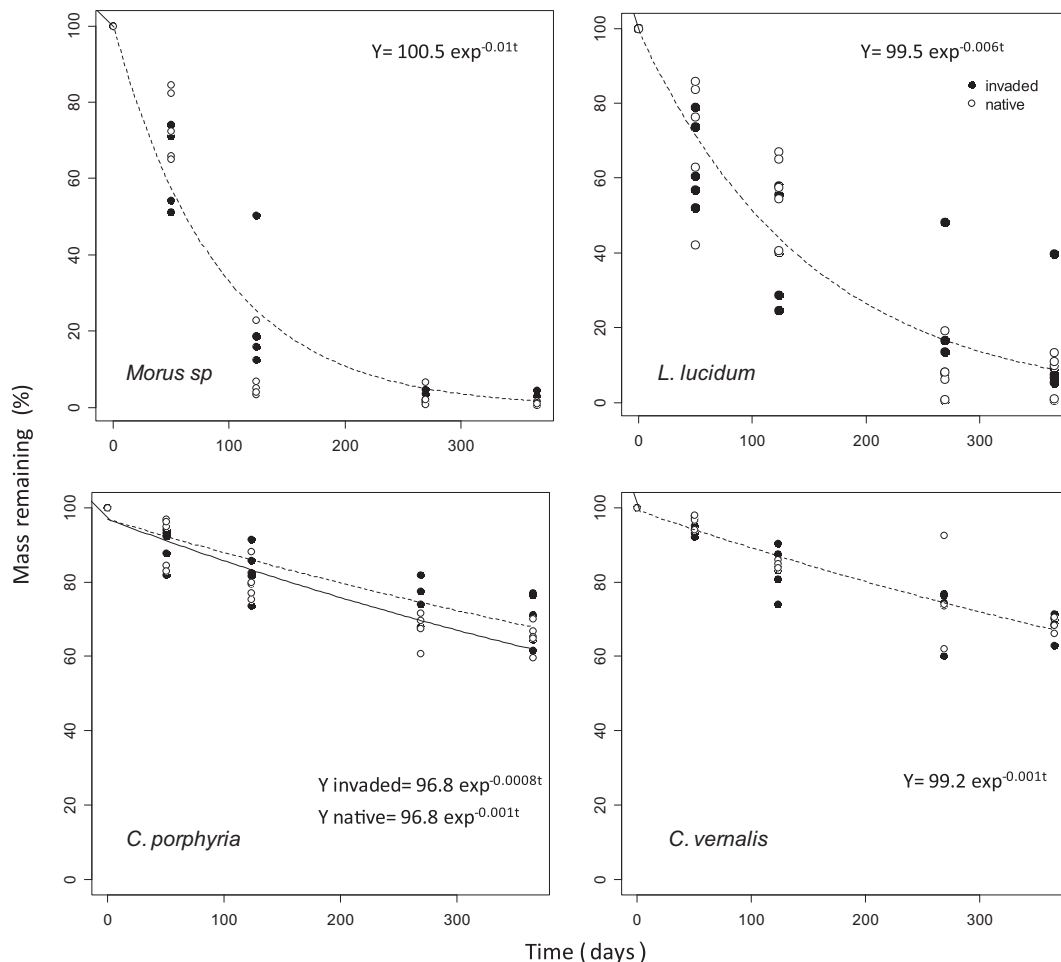


Fig. 2. Percentage of mass remaining through time in *Ligustrum*-dominated and native stands. Curves represent negative exponential models adjusted by maximum likelihood. In the case of *C. porphyria* the model with different slopes for distinct forest types had a better fit (solid: invaded sites, dashed: native sites) than a common model for both forest types.

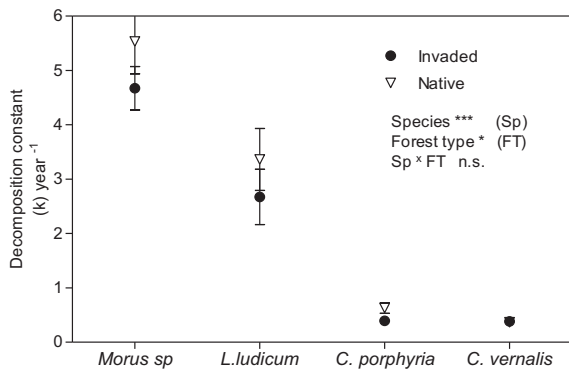


Fig. 3. Decomposition constants (k) calculated using a linear model of log-transformed data for each species in invaded and native sites. Means and standard errors are presented. *** $p < 0.001$, * $p < 0.05$.

However, the more complex model which considered different slopes for distinct forest types had a significantly better fit only for *C. porphyria* ($\Delta AIC = 3.5$) (Fig. 2). In this case, the slope describing the decomposition function in native forests was 10% steeper than that of *Ligustrum* forests stands. Decomposition constant (k) of *C. porphyria* in native forest stands was 30% higher than in *Ligustrum* forest stands. In all other species, the difference between the slopes of decomposition curves for both forest types was no more than 5%, and including different slopes in the models did not represent a significant improvement.

3.2. Physical and chemical leaf litter traits

Specific leaf area (SLA) differed among species ($F_{3,16} = 127.39$, $p < 0.01$) but this difference was not explained by the differences between exotic and native species (Table 2). *L. lucidum* SLA was similar to that of natives, while *Morus sp.* showed the highest SLA. Litter water content was lower in *L. lucidum* (K.W. = 18.09, $p < 0.01$), but there was no difference among *C. porphyria*, *C. vernalis* and *Morus sp.* Again, the pattern was not associated with their exotic/native status. All the species, except *Morus sp.*, showed similar tensile strength. *Morus sp.* tensile strength was 30% that of the rest of the species ($F_{3,10} = 18.66$, $p < 0.01$) (Table 2).

Species differed in N and C content ($F_{3,17} = 2.41$, $F_{3,17} = 36.87$, $p < 0.01$ for N and C respectively). *L. lucidum* and *Morus sp.* had the lowest and highest values in N content, respectively. In addition, *Morus sp.* had the lowest C content, followed by *L. lucidum*. Both had significantly lower %C than that of natives (Table 2). *Morus sp.* and *L. lucidum* showed the maximum and minimum C:N ratio, respectively ($F_{3,17} = 41.29$, $p < 0.01$). *C. vernalis* and *C. porphyria* showed intermediate values, and consequently, the pattern in C:N ratio was not associated to the species exotic/native status.

3.3. Environmental variables in *Ligustrum* dominated and native forest stands

L. lucidum stands showed decreased soil humidity but similar soil temperature than native stands. The soil of *Ligustrum* forests

Table 1

Decomposition constants (k) (mean and standard errors), T_{50} and T_{95} (time in years required for 50% or 95% litter weight loss) for each species averaged across forest types.

Species	k	T_{50}	T_{95}
<i>Morus sp.</i>	5.104 ± 0.49	0.135	0.587
<i>L. lucidum</i>	3.018 ± 0.53	0.229	0.993
<i>C. porphyria</i>	0.512 ± 0.06	1.352	5.855
<i>C. vernalis</i>	0.375 ± 0.03	1.847	7.998

was consistently drier than that of native forests, and this difference was approximately constant during all the sampling dates ($F_{1,4}$ forest type = 10.43, $p = 0.03$; $F_{3,24}$ time = 86.99, $p < 0.01$; $F_{3,24}$ forest type*time = 0.7, $p > 0.5$) (Fig. 4). Soil temperature did not differ between forest types, but varied seasonally, as expected ($F_{2,16}$ time = 123.52, $p < 0.01$).

4. Discussion

The four species under study differed in their decomposition rates. Exotic species decomposed more rapidly than natives. In addition, three out of the four species tended to have lower decomposition rates in *Ligustrum* forests. However, largest differences in decomposition were observed among species rather than between forest types.

L. lucidum invasion can affect organic matter dynamics on the forest floor in the mountain forests of NW Argentina through several mechanisms. First, *L. lucidum* has a relatively abundant leaf production (Dascanio et al., 1994; Ayup, unpublished data) and a profuse litter fall. Second, as our results show, its litter quickly decomposes. Consequently, when *L. lucidum* becomes abundant in a secondary forest stand, litter inputs to the forest floor increase, as well as, overall litter decomposability. Nutrients are thus expected to become more rapidly available to plants in *Ligustrum* forest stands. This may have an important effect on the primary productivity of invaded sites, and may partially explain *L. lucidum* high growth rates (Easdale et al., 2007). *L. lucidum* elevated decomposition rate also explains the reduced thickness of the litter layer in *Ligustrum* forests (Ayup et al., this issue), even though it has an abundant leaf production.

Once *L. lucidum* becomes dominant, the canopy cover gets denser, and light availability, as well as soil humidity, are reduced (Lichstein et al., 2004; Zamora, 2012; Ayup et al., this issue). Water availability affects rates of mass loss and nutrient release primarily through its effects on the activity of the decomposer community (Meentemeyer, 1978; Orchard and Cook, 1983; Berg, 1986). Decreased light availability and soil moisture are expected to slow decomposition processes (Cortez and Bouché, 1998; Austin and Vivanco, 2006). However, decomposition in *Ligustrum* forest was significantly slower only in the case of *C. porphyria*. Consequently, litter type remains as the main control of litter decomposition rates in these forests, in spite of the modified environmental conditions (i.e., reduced light and humidity) associated with *L. lucidum* invasion (Lichstein et al., 2004; Ayup et al., this issue).

The annual rate of decay for both exotics in our study area was significantly higher than that of native species. Importantly, *Morus sp.* and *L. lucidum* decomposition rates showed particularly high values considering data from other subtropical (Arunachalam et al., 1996) and even tropical species (Aerts, 1997; Powers et al., 2009). However, decay rates of native species were rather low in relation to other tropical forest species ($k = 1.25$ was the most common value in Powers et al., 2009). *L. lucidum* rate of decay in our study was slightly lower than the value found by Dascanio et al. (1994) for litter in riparian forests of Eastern Buenos Aires province, Argentina. This difference may be due to the frequent floods that affect riparian forests, which can promote litter decomposition. Furey (2010) assessed decomposability of several exotic and native species in the mountain dry forest of Córdoba province, Argentina, including *L. lucidum* and *Morus alba* litter. The percentage of litter remaining after 45-day of incubation in this dry forest ecosystem (45% and 70% for *Morus alba* and *L. lucidum*, respectively) were similar to those found in our study. Also in agreement with our results, *M. alba* showed one of the highest decomposition rates when compared with the rest of the native and exotic species in that area. This could be explained by *Morus sp.* leaf attributes

Table 2
Initial leaf litter characteristics (Mean \pm standard errors). Different letters indicate differences at $p < 0.05$. SLA: specific leaf area.

Leaf characteristics	Invasive		Native	
	<i>Morus</i> sp.	<i>L. lucidum</i>	<i>C. porphyria</i>	<i>C. vernalis</i>
SLA ($\text{mm}^2 \text{gr}^{-1}$)	20.29 \pm 1.30 b	10.37 \pm 1.94 a	10.29 \pm 0.54 a	9.95 \pm 0.51 a
Litter water content	13.55 \pm 0.29 bc	5.83 \pm 0.89 a	10.95 \pm 0.60 b	12.58 \pm 0.77 bc
Tensile strength (N mm^{-1})	0.52 \pm 0.03 b	0.75 \pm 0.02 a	0.78 \pm 0.03 a	0.73 \pm 0.03 a
N (%)	2.36 \pm 0.25 c	0.82 \pm 0.03 a	1.28 \pm 0.10 ab	1.83 \pm 0.07 bc
C (%)	37.87 \pm 0.77 a	44.12 \pm 1.21 b	50.46 \pm 1.38 c	49.65 \pm 0.47 c
C:N	16.90 \pm 1.93 a	53.72 \pm 2.40 d	40.57 \pm 4.13 c	27.15 \pm 0.86 b

(i.e., high SLA, low tensile strength and low C:N ratio), that are generally associated with high decomposability (Cornelissen et al., 1999; Pérez-Harguindeguy et al., 2000).

As we previously mentioned, species with pioneer characteristics are considered the most successful invaders in woody ecosystems (Baruch and Goldstein, 1999; Allison and Vitousek, 2004; Funk and Vitousek, 2007). In this study we found that *Morus* sp. shows many leaf characteristics that are generally related to high growth rate (i.e., high SLA, low tensile strength, low C:N, high decomposition rate) and pioneer status. Conversely, *L. lucidum*, which is the most abundant exotic species in this area, shares some leaf attributes with the native late successional species, *C. porphyria* and *C. vernalis*, but shows significantly higher decomposition and growth rates. *L. lucidum* may also differ from natives in other leaf attributes that were not measured here (e.g. lignin content). Importantly, *L. lucidum* also has late successional characteristics (e.g., shade tolerance, high competitive ability). This indicates that successful invaders do not necessarily have attributes of pioneer species.

Morus sp. has leaf traits commonly found in woody invasive species (thin, tender, nutrient rich leaves) that show an acquisitive pattern of resource use (Diaz et al., 2004; Leishman et al., 2007; Ehrenfeld, 2010; Tecco et al., 2010). Due to its characteristics (high SLA and nutrient content, fast decomposition rate) *Morus* sp. could be placed in the fast- return end of the “leaf economics spectrum”, as it happens with many successful invaders (Peñuelas et al., 2010). According to our results, the placement of *L. lucidum* in the leaf economy spectrum is less clear. Its leaves are relatively tough, have intermediate SLA values, and are nutrient poor (high C:N). However, contrary to our expectations, they decompose fast compared to native species (more than 5 times faster than *C. vernalis* and *C. porphyria* litter). It is important to highlight that in this study, we measured physical and chemical attributes on senescent leaves. If green leaves had been considered, the patterns we found could

have been different because of nutrient translocation or differential dehydration. Measurements of these traits (especially SLA and tensile strength) on senescent leaves are not strictly comparable with measures from green leaves (see Appendix for SLA measurements on green leaves). This has to be taken into account when comparing our results with trait values reported in other studies. In addition, we are aware that even though in many cases C:N ratio explains the decomposition rate (Tian et al., 1992; Aerts, 1997), other chemical properties of the litter not considered in our study, such as lignin, lignin: N or P concentration may be influential as well. There is evidence that other species of the same genus (*Ligustrum sinensis*) has relatively low concentration of lignin and cellulose, and a C:N ratio similar to that of *L. lucidum* (Mitchell et al., 2011). If *L. lucidum* leaves had similar chemical composition than those of *L. sinensis*, this could explain its high rate of decay. However, differences in life form (tree versus medium height shrub) among these species may limit this comparison.

In addition, we would like to remark that litter from different species was incubated at the same time in our experiment. Although senescent leaves of the four species naturally co-occur in the forest floor, the timing of litterfall further influences decomposition. *Morus* sp. is a deciduous species, with litterfall sharply concentrated during the autumn, while *L. lucidum* has two peaks in litterfall (in autumn and spring) (Dascanio et al., 1994). Litterfall in *C. porphyria* and *C. vernalis* is more evenly expanded throughout the year (Boletta et al., 1995). Consequently, invasion by exotic species may influence the rate of nutrient release at ecosystem level, not only by changing litter quantity and quality, but also by affecting the timing of leaf inputs to the forest floor.

We would also like to point out two aspects of our experiment which should be taken into account when interpreting its results. First, leaves from each species were incubated in different litter bags. This was necessary to discriminate patterns of weight loss between the different species. However, we are aware that litter diversity may enhance decomposer diversity and activity, and that, in turn, may affect decomposition (Gartner and Cardon, 2004; Freschet et al., 2012). Second, we did not specifically control the identity and diversity of the species in the adjacent area of the experimental plots. In some cases, it was shown that decomposition is affected by the identity of neighboring tree species (Vivanco and Austin, 2008; Freschet et al., 2012). While *L. lucidum* was the most common tree in the canopy of invaded stands, native sites were more diverse (Lichstein et al., 2004). Effect of neighboring canopy trees on the decomposer community, or the interaction between substrate quality in the litter bags and litter in the surrounded matrix can substantially affect decomposition rates (Freschet et al., 2012). This may account for the variation in decomposition between litter samples of the same species in different sites within the same forest type.

Finally, our work highlights two aspects that should be considered when comparing the ecosystem- level impacts of exotic species in native communities. First of all, the comparison between exotic and native species should include more than one species,

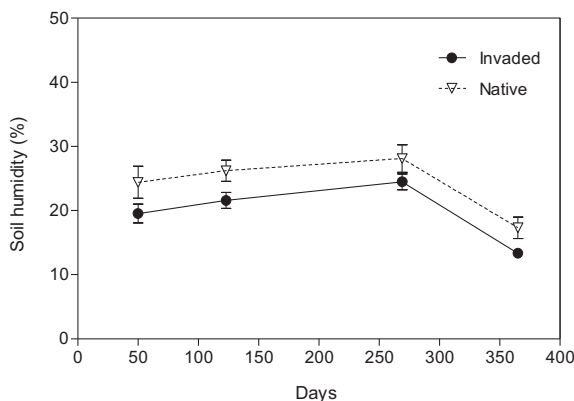


Fig. 4. Mean percentage of soil humidity in *Ligustrum*-dominated and native stands in the four sampling periods. Bars represent standard errors.

since exotics, even pioneer ones, may have varying traits values. And second, species effects on ecosystem processes can be determined by their relative abundance. This study suggests that even though decomposition rate of *L. lucidum* is not as high as *Morus* sp. rate, this species is having a prominent impact on nutrient cycling because of its dominance. Secondary forests of Sierra de San Javier offer a very convenient set up for future research, since 15 exotic tree species with a multiple range of attributes (e.g., height, shade tolerance, type of dispersion mode) and abundances coexist in this diverse forest area (Grau and Aragón, 2000). Examining a broader set of species and comparing species traits and decomposability in a common environment are interesting avenues for future research.

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Appendix A. SLA (Mean \pm standard errors) measurements on green leaves. Different letters indicate differences at $p < 0.05$.

Species	SLA ($\text{mm}^2 \text{gr}^{-1}$)
<i>Morus</i> sp.	17.55 \pm 0.36 b
<i>L. lucidum</i>	14.35 \pm 0.30 a
<i>C. vernalis</i>	13.84 \pm 0.34 a
<i>C. porphyria</i>	14.38 \pm 1.70 a

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