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***Ligustrum lucidum* invasion decreases abundance and relative contribution of soil fauna to litter decomposition but increases decomposition rate in a subtropical montane forest of NW Argentina**

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Abstract

Invasive plant species can alter litter decomposition rates through changes in litter quality, environment conditions and decomposer organisms (microflora and soil fauna) but limited research has examined the direct impact on soil fauna. We assessed the abundance and relative contribution of soil meso- and macrofauna to litter decomposition in invaded forest by *Ligustrum lucidum* and non-invaded forest in a subtropical mountain forest of northwest Argentina using litterbags (0.01, 2 and 6 mm mesh size). Additionally, we analyzed litter quality and soil properties of both forest types. Soil fauna abundance was lower in invaded than in non- invaded forest. The contribution of soil macrofauna to litter decomposition was important in both forest types, but soil mesofauna contribution was only significant in non-invaded forest. Litter decomposition was significantly faster in invaded than in non-invaded forest, consistent with its highest quality. Invaded forest had significantly lower litter accumulation, lower soil moisture and greater soil pH than non-invaded forest. Our results showed that, although soil fauna was less abundant and played a less pronounced role in litter decomposition in invaded forest; these changes did not translate into a reduced litter decomposition rate due to the higher quality of litter produced in the invaded forest.

Keywords: glossy privet, invasive alien species, litter decomposition, soil meso- and macrofauna, Subtropical montane forest

Introduction

One of the characteristics of the Anthropocene is that no place seems immune to biological invasions. Invasion by alien species is, in fact, considered one of the main drivers of the global alteration of ecosystems (Vilá et al. 2011; IPBES 2019). Several studies have documented that invasive alien plants can change species composition, diversity, and community structure (e.g. Vilá et al. 2011; Castro Diéz et al. 2016) and alter ecosystem processes such as litter decomposition rate and nutrient cycling (e.g. Liao et al. 2008; Godoy et al. 2010; Aragón et al. 2014; Castro-Díez et al. 2014). The impacts of invasive alien plants on litter decomposition are related to changes in the three key drivers of this process: litter quality, microenvironment conditions and decomposer organisms (i.e. microflora and soil fauna). Several studies compared the characteristics of the litter quality produced by invasive alien plants and native plants and have found differences between them which had consequences in the litter decomposition rates of invaded ecosystems. For example, according to some studies, litter of invasive alien plants had higher N content than litter of native species which accelerated decomposition rates in a wide range of the invaded ecosystems (Liao et al. 2008; Castro-Díez et al. 2009). In contrast, other studies found that litter produced by invasive alien plants had higher C:N ratio or lignin content which slowed down litter decomposition rate in temperate grasslands and in a wide range of the invaded systems (Godoy et al. 2010; Mincheva et al. 2014). Additionally, invasive alien plants can alter the quantity and timing of litter production on invaded ecosystems (Ehrenfeld 2003). Differences in litter quality and quantity may not only affect decomposition rate directly but also indirectly, by altering the available food resources and habitat structure for soil fauna (Ehrenfeld 2003; Abgrall et al. 2019). Previous studies also found that when invasive alien plants differ in phenology and canopy density from native species (for example, by increasing canopy cover in more open natural vegetation) they can cause significant changes in light availability and soil properties (e.g. moisture, pH and soil organic matter content) in invaded ecosystems (Vilà et al. 2011; Aragón et al. 2014). All these changes in litter quality, quantity and environmental conditions, can modify species composition, abundance and activity of soil fauna which in turn can further alter the decomposition rate in invaded ecosystems due to its important role in this process (Schädler and Brandl 2005; Powers et al. 2009; Abgrall et al. 2019). There is growing evidence that invasive alien plants have negative impacts on soil fauna abundance (Gerber et al. 2008; Gutiérrez-López et al. 2014; Motard et al. 2015; Sterzyńska et al. 2017; Woodworth et al. 2020). However, results of a meta-analysis found that soil fauna abundance may also increase following plant

invasions (Abgrall et al. 2019). Despite the recognition of the impact of plant invasions on soil fauna, studies evaluating how these impacts affect the litter decomposition rate are still scarce.

In this study, we quantified the abundance and relative contribution of soil meso- and macrofauna to litter decomposition in invaded forest by *Ligustrum lucidum* (“glossy privet”, Oleaceae) and non-invaded forest in a subtropical mountain forest of northwest Argentina. *L. lucidum* is an evergreen tree native from China considered an invasive species in many countries around the world with noticeable negative impacts on native biodiversity and some ecosystem services (e.g. water regulation) (Fernandez et al. 2020). *L. lucidum* is one of the most important invasive alien trees in northwest and central Argentina, where it forms monospecific forest stands (Montti et al. 2017; Fernandez et al. 2020). Previous studies have shown that the forest invaded by *L. lucidum* (hereafter “invaded forest”) in northwest Argentina produced lower litter quantity than the non-invaded forest since it is dominated by *L. lucidum* which is an evergreen species, while the non-invaded forest is dominated by deciduous or semi-deciduous native species (Aragón et al. 2014; Ayup et al. 2014).

Additionally, leaf litter produced by *L. lucidum* showed higher quality than leaf litter produced by dominant native species (Aragón et al. 2014). According to other studies the differences on leaf litter quality produced by *L. lucidum* and by native species has been proposed to explain the reduction of the abundance of fungal decomposers and the changes on their composition and activity of fungal communities (Fernandez et al. 2017; Mallerman et al. 2018). All those changes on leaf litter quantity and quality and fungal decomposers could alter food resources and habitat structure for soil fauna, affecting litter decomposition rate. Given that the invaded forest produces lower leaf litter quantity and shows a lower abundance of fungal decomposers than non invaded forest, we expect to find lower soil fauna abundance (meso- and macrofauna) in invaded than in non-invaded forest. Although the exclusion of any soil fauna group could significantly decrease litter decomposition, we expect this effect to be more pronounced in invaded than in non-invaded forest.

Additionally, we analyzed the quality of leaf litter mixtures from invaded and non-invaded forest (measure as decomposability) in a common garden experiment and we measured soil parameters (soil moisture and litter depth, soil pH, soil organic matter and soil nitrogen content) *in situ* in both forest types. Given the dominance of *L. lucidum* in the invaded forest, we expect the quality of leaf litter mixtures from this forest show of higher than leaf litter mixtures from non-invaded forest. Also, according to the differences in phenology and timing of leaf litter production in invaded (evergreen forest) and non-invaded forest (semi- deciduous); we

expect lower soil moisture and litter depth in invaded than in non-invaded forest.

Methods

Study area

The study was carried out in Parque Sierra de San Javier (26°70'S, 65°35'W) a protected area in Tucuman province, Argentina. The native vegetation is a semi-deciduous mountain forest of the Neotropical Andean mountain forests, also known as “Yungas” (Cabrera 1976). Annual rainfall is 1200 mm (90% falls during the summer in the Southern Hemisphere) and average annual temperature is 18°C (Bianchi and Yañez 1992). Many areas of the lower mountain forest were deforested for agriculture (mainly citrus and sugar cane crops) and grazing during the early twentieth century (Grau et al. 1997). However, in the last two decades many agricultural fields have been abandoned and currently show different forest regeneration stages (Grau et al. 2008). Most secondary forest patches are dominated by native species but some have been invaded by *L. lucidum* (Grau et al. 2008). Non-invaded and invaded forests differ in vegetation structure and species composition. Non-invaded forest exhibit three strata: a canopy, dominated by tree species such as *Ocotea porphyria*, *Blepharocalyx salicifolius* and *Cupania vernalis*; a subcanopy, dominated by *Piper tucumanun*, *Eugenia uniflora* and *Allophylus edulis*; and an understory, dominated by the shrub *Psychotria carthagenensis* (Malizia et al. 2010). By contrast, invaded forest exhibit lower diversity of trees, shrubs and lianas species (Aragón and Morales 2003; Lichstein et al. 2004) and a simplified vertical structure, with a canopy dominated by *L. lucidum* and an understory dominated by *P. carthagenensis* (Lichstein et al. 2004).

In situ litter decomposition experiment

We used a paired design with 5 sites for each forest category (5 invaded non-invaded forest pairs). Sites were selected based on their similarity in age (between 30 and 50 years of succession), altitude (between 630 and 780 masl), soil type (Entisol), and land-use history (agriculture). The distance between each pair of sites ranged from 200 to 500 m. In each site we randomly established a 20 x 20 m plot and collected recently fallen leaf litter mixtures from March 2013 to March 2014 using cotton fabric pieces suspended above the soil as leaf traps. Leaf litter mixtures from invaded forest were dominated by the leaf litter of *L. lucidum*, whereas leaf litter mixtures from non-invaded forests were composed by leaf litter of several native species (e.g. *O.*

141 *porphyria*, *B. salicifolius*, *C. vernalis*, *P. tucumanun* and *A. edulis*). Leaf litter mixtures were air-dried and
142 stored in open paper bags until further analysis.

143 In order to evaluate the relative contribution of meso- and macrofauna to litter decomposition in invaded and
144 non-invaded forests we conducted an *in situ* litter decomposition experiment. For this experiment, that is a
145 soil fauna exclusion experiment, we used litterbags (20 x 20 cm) with three mesh sizes: small mesh (0.01
146 mm) which excluded access for both meso- and macrofauna, medium mesh (2 mm), which excluded access
147 for macrofauna and large mesh (6 mm), which permitted access of all soil fauna (Swift et al. 1979; Petersen
148 and Luxton (1982); Bradford et al. 2002). All mesh sizes allowed the access of microflora. A total of 180
149 litterbags were used (2 litterbags x 3 mesh sizes x 5 sites x 2 forest types x 3 harvest times (30, 90 and 180
150 days) = 180 litterbags) with 2.00 ± 0.01 g litter mixtures in each of them. They were placed on September 15,
151 2014 on the soil surface in each of the 5 sites of each forest type. We collected the litterbags at 30, 90 and 180
152 days from the beginning of the experiment and transported them to the laboratory in paper bags for
153 processing.

154 Before litter processing, we extracted the soil fauna by placing the remnant litter from each litterbag of 2 and
155 6 mm mesh size in Berlese–Tullgren funnels for 4 days illuminated by 20W lamps. The soil meso- and
156 macrofauna collected were preserved in 70% ethanol and all adult individuals were identified to order level,
157 except Acari that were identified at subclass (Borror et al. 1997; Momo and Falco 2009). Coarser level
158 identification approach allows the assessment of broader community trends and is particularly useful when
159 taxonomic knowledge is limited (e.g. Araujo et al. 2012; Marichal et al. 2014). After soil fauna extraction, the
160 remaining litter of all litterbags (0.01, 2 and 6 mm mesh) was carefully cleaned by removing soil, dried at
161 60°C to constant weight and weighed. Litter decomposition was calculated as the difference between initial
162 litter mass and final litter mass after incubation and was expressed as % litter mass loss.

164 **Common garden experiment**

165 We used decomposability as an integrated measure of the quality of leaf litter mixtures for decomposers.
166 Decomposability is considered an integral expression of litter quality (Pérez-Harguindeguy et al. 2013) and
167 can be assessed by common garden experiments where different substrates are placed under the same
168 incubation conditions (i.e., soil temperature, soil humidity, soil decomposer community). These conditions

ensure that any given differences in decomposition rates can be attributable to differences in litter quality (Pérez-Harguindeguy et al. 2013). We carried out a common garden experiment to evaluate the decomposability of leaf litter mixtures produced by invaded and non-invaded forests. We prepared litterbags with 2 mm mesh containing 2 ± 0.1 g of recently fallen leaf litter mixtures collected in each forest type (3 litterbags x 5 sites x 2 forest types x 3 harvest times (30, 90 and 180 days) =90 litterbags). They were then placed in a decomposition bed 5×4 m constructed in the garden of the Institute of Ecology Regional (IER), within the study area under the same standard conditions of climate, vegetation, soil properties and decomposer organisms (Fig. 1). This ensures that there is no field advantage for any treatment (i.e. litter from invaded and non-invaded forests). All litterbags were placed on the soil surface of the decomposition bed with at least 10 cm apart on September 15, 2015. We collected the litterbags at 30, 90 and 180 days from the beginning of the experiment and transported them to the laboratory in paper bags for processing the litter in the same way that the in situ leaf litter decomposition experiment.

Characterization of soil properties

In order to evaluate soil properties of invaded and non-invaded forests we measured soil moisture and litter depth in the same plots where the litterbags were placed (Fig. 1). We estimated soil moisture using three 10 cm deep soil cores taken in each plot at the same time we collected litterbags. 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. We determined litter depth by placing a ruler perpendicular to the soil in 10 randomly selected points at each plot and at every harvest time (30, 90 and 180 days). We also measured soil pH, soil organic matter (SOM) and soil nitrogen (N) contain (%) from a composite soil sample of three sub-samples taken within each site in March 2015 (wet season; summer) and August 2015 (dry season; winter). Soil pH was determined using a soil-water ratio of 1:5, SOM was determined by calcination, and soil N content was evaluated by the Kjeldahl method as described by Page et al. (1982).

Data analysis

To compare soil fauna abundance (individuals per sample) between forest types we used generalized linear mixed models with binomial error distribution to account overdispersion with the *lme4* R package (Bates et al.

2015). To evaluate the relative contribution of meso- and macrofauna to decomposition of leaf litter mixtures produced and incubated under invaded and non-invaded forest we used linear mixed models with the *nlme* package (Pinheiro et al. 2020). In each model, forest type (invaded and non-invaded), mesh size of litterbags (0.01 mm; 2 mm and 6 mm), time and their interactions were considered fixed factors while time and sites were considered random factors. Similarly, litter decomposability was analyzed by generalized linear mixed models using forest type, time and their interactions as fixed factors and time and sites as random factors. We removed non-significant interactions between fixed effects to obtain the most parsimonious model. When full models were significant, we performed pairwise comparison with the *emmeans* R package (Lenth et al., 2020) in order to test which treatments caused the previously observed differences. Regarding soil parameters (soil moisture, litter depth, soil pH, SOM and soil N contain) we used linear mixed models with forest type, time and their interactions as fixed factors and sites as random factor. When necessary a VarIdent variance structure was used to account for heteroscedasticity. All statistical analyses were conducted using R 3.5.0 (R core team 2018).

Results

Soil fauna

We collected a total of 2075 and 3323 individuals in invaded and non-invaded forest respectively, belonging to 13 different taxa (Table A1). Acari and Collembola were the most abundant groups, comprising more than 90% of the total individuals collected. Soil fauna abundance (meso- and macrofauna) was significantly 55% lower in invaded than in non-invaded forest in litterbags with 2 and 6 mm mesh sizes (Table 1, Fig. 2). However, the effect of forest type depended on mesh size and time (significant interaction forest type $\times$ mesh size $\times$ time, Table 1). At the beginning of the experiment, both forest types showed greater soil fauna abundance (58% and 23 % in invaded and non invaded forest respectively) in litter from 2 mm litterbags (only mesofauna) than in litter from 6 mm litterbags (with meso- and macrofauna) (Figure 1). But on the last experiment date (180 days), total abundance was 45% greater in litter from bags of 2 mm mesh size than in litter from bags of 6 mm in non-invaded forest, whereas this difference was only 3 % in invaded forest (Fig. 2).

***In situ* litter decomposition experiment**

Forest type, litterbag mesh size, and time all had a significant effect on litter decomposition rate (Fig. 3, Table 2). The effects of forest type on decomposition depended on time and on the litterbag mesh size (Table 2). As decomposition progressed differences in decomposition rate between forest types and among different mesh sizes increased (Fig. 3, Table 2, Table A2). The effects of mesh size also depended on time (Table 2). Mesofauna access did not significantly affect litter decomposition rate in invaded forest but was significant for litter decomposition rate in non-invaded forest (Table 2, Fig. 3, Table A3). In general, in litterbags of larger mesh size (6 mm mesh size, with meso- and macrofauna access) litter decomposition was higher than in litterbags of 2 mm, but the magnitude of that effect was smaller in the invaded than in non-invaded forest. Compared to the 2 mm bags, the litter mass loss (%) in the 6 mm bags, with soil meso- and macrofauna access was 3% and 18% higher in invaded and non-invaded forest respectively.

Common garden experiment and soil properties

As decomposability progresses over time, differences in mass loss (%) between litter mixtures from different forest types increase (forest type $\times$ time, $F=69.99$; $p<0.0001$; Fig. 4). At the end of the experiment (180 days), decomposability of litter mixtures from invaded forest was 27% higher than that of the non-invaded forest (Fig. 4).

Regarding soil properties, invaded forest had significantly lower soil moisture ($F= 35.08$; $p<0.0001$), litter depth ($F= 1593$; $p<0.0001$) and significantly higher soil pH ($F= 16.95$, $p=0.02$) than non-invaded forest (Table 3).

Discussion

Our results showed that in forest invaded by *L. lucidum* in subtropical mountain forest soil fauna was significantly less abundant and played a reduced role on litter decomposition than in non- invaded forest. Importantly, these changes did not translate into a slower litter decomposition rate in the invaded forest. In fact, leaf litter mixtures from invaded forest decomposed faster than leaf litter mixtures from non-invaded forest, probably because of its highest litter quality.

According to the hypothesis of Woodworth et al. (2020) that claimed that native habitats support a greater abundance of arthropods than invaded ones because of leaf litter quantity that reaches the soil, we found higher abundances of soil meso- and macrofauna in non-invaded than in invaded forest. These results are consistent with those found in habitats invaded by other alien plants such as *Fallopia* sp, a perennial herbaceous species, invading riparian grasslands and shrubs in Europe (Gerber et al. 2008), and *Ailanthus altissima*, a semi-deciduous tree invading riparian forest of Spain (Gutiérrez-López et al. 2014; Motard et al. 2015). This suggests that, independently of the life form of the invasive alien plants (i.e. tree, herbaceous) and the dominant physiognomy of the invaded environment (i.e. forest, grassland), the pattern of lower soil fauna abundance in invaded sites is recurrent. This pattern is confirmed by a meta-analysis that includes invasive alien plants with different life-forms (i.e. herbaceous, trees) and in a variety of vegetation communities (i.e. forest tropical savanna, riparian forest, scrubland, salt marsh, grassland), which showed that, overall, invaded habitats had a 29% lower arthropod abundance compared to non-invaded habitats (van Hengstum et al. 2014). Generally, changes of soil fauna abundance in invaded habitats can be explained by changes in litter quality or in microenvironment conditions caused by invasive alien plants (Gutiérrez-López et al. 2014; van Hengstum et al. 2014; Motard et al. 2015). Our results showed that litter quality was not the driver of reduced soil fauna abundance, as litter decomposability (our integral proxy for litter quality) was highest in leaf litter mixtures from the invaded forest, which presented the lowest soil fauna abundance. Regarding the microenvironment conditions, previous studies suggested that greater abundance of soil meso- and macrofauna could be connected to soil parameters such as higher litter depth, soil moisture and soil pH (Rusterholz et al. 2014; Sterzyńska et al. 2017). In line with this, we found greater abundance of soil meso- and macrofauna in non-invaded forest that had higher soil moisture and litter depth in comparison with invaded forest. A lower litter depth in invaded forest not only reduces food resources and microhabitats for soil fauna, but also reduces the efficacy of litter as a barrier to attenuate microclimate conditions (i.e., temperature or moisture) and to protect soil fauna from predators (Ashford et al. 2013; Perez et al. 2013). Also, previous studies found that lower soil moisture decreased the soil fauna activity and diversity which affected the contribution of soil fauna to litter decomposition (Riutta et al. 2016; Tan et al. 2020). According to this in our case the lower soil moisture in the invaded forest may negatively affect soil fauna and their contribution to litter decomposition. Finally, it should be noted that the abundance of soil mesofauna was

higher in litter from bags of 2 mm mesh size, which excluded macrofauna, than in litter from larger mesh size litterbags (6 mm), where the soil meso- and macrofauna accessed. A possible explanation for this finding could be a higher macrofauna predator pressure in the larger mesh size litterbags.

Regarding the role of soil fauna to litter decomposition, the exclusion of the soil meso- and macrofauna (in 0.01 mm mesh size litterbags) negatively affect litter decomposition rates in our study area. This pattern is typically associated with the soil meso- and macrofauna in the litter breakdown and hence in the increase of the surface area of the resource that facilitates the access for microbial decomposers (Frouz 2018). However, the effect of the exclusion was weaker, and even not significant for soil mesofauna in invaded forest, consistently with the lower abundance of soil fauna in this forest type. A plausible explanation for the greatest relative contribution of soil meso- and macrofauna to litter decomposition in non-invaded forest could be the lower quality of its litter. Soil fauna has a more important role on litter decomposition rate in habitats dominated by litter of poor quality because fragmentation and consumption by soil fauna represents a crucial step that allows the access of microorganisms (Milcu and Manning 2011; Gergocs and Hufnagel 2016). By contrast, microflora (i.e. bacteria and fungi) and microfauna (which is typically dominated by protozoa and nematodes) seems to have an important contribution to the litter decomposition process in both forest types, as was indicated by the important litter mass loss (%) in litterbags with 0.01 mm mesh size (Fig. 3). This result is not surprising since litter decomposition has been consistently reported as mainly driven by the activity of the microflora, while the effect of soil fauna has been shown to vary between experiments and habitats (González and Seastedt 2001; Powers et al. 2009).

Despite the abundance of meso- and macrofauna and their contributions to litter decomposition were lower in invaded than in non-invaded forest, leaf litter mixtures from invaded forest decomposed more quickly. This highlights the relatively more important role of another driver of decomposition rate in this subtropical forest ecosystem: litter quality. These results are in line with the review of the drivers of decomposition proposed by Zhang et al. (2008) in which litter quality emerges as the driver with a more predominant importance at multiple scales than previously thought (e.g. Swift et al. 1979; Aerts 1997). Our results also coincide with a previous study involving other tree invaders and found that the abundance of soil fauna is not a good indicator of the decomposition rate and that the higher quality of litter mixtures of invaded forest greatly explained its decomposition rate (Bedano et al. 2014). Alternatively, litter may have decomposed faster

in the invaded forest not only because of the highest litter quality, but also because the soil fauna was more efficient at decomposing leaf litter produced there since previous studies have demonstrated the decomposer organisms can be specialized to some types of litter (e.g. Wardle 2006; Vivanco and Austin, 2008; Ayres et al., 2009). It is possible that specialization of the decomposer community be facilitated by litter homogeneity in invaded forest (mostly dominated by *L. lucidum* litter). However, further studies would be needed to assess if this occurs in our study area.

Conclusions

Soil fauna is a one of the key drivers on litter decomposition and could be affected by plant invasions, however, its role had received little attention compared to other drivers of litter decomposition, and in particular it had not been considered in the context of *L. lucidum* invasion (Fernandez et al. 2020). Our study provides the first evidence of the effect of *L. lucidum* on soil fauna abundance and its contribution to litter decomposition in a subtropical mountain forest of NW Argentina. We showed that at a local scale the soil meso- and macrofauna abundance and their relative contribution to leaf litter decomposition was lower in invaded than in non-invaded forest. However, we observed a higher litter quality and a higher litter decomposition rate in invaded compared to non-invaded forest. Taken together, our results indicate that although soil fauna was less abundant and played a less pronounced role in the litter decomposition in invaded forest; these changes did not translate into a reduced litter decomposition rate due to the higher quality of litter produced in the invaded forest.

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Figures

Fig 1. Graphic diagram of the experiments carried out in this study; a) *in situ* litter decomposition experiment, b) Common garden experiment and c) characterization of soil parameters.

Fig. 2. Soil fauna abundance (number of individuals per sample) in invaded (circles) and non-invaded forest (squares). Squares and circles represent mean values of soil fauna abundance over time ($\pm$ SE, $n = 5$) in each mesh sizes of litterbags: 2 mm (macrofauna exclusion, gray), and 6 mm (no soil fauna exclusion, with light gray) in each forest type.

Fig. 3. *In situ* litter decomposition (% litter mass remaining of litter mixtures incubated in the same plots where it was collected) in invaded (circles) and non-invaded forest (squares). Squares and circles represent mean values of litter mass remaining over time ($\pm$ SE, n = 5) for each mesh size of litterbag: 0.01 mm (meso- and macrofauna exclusion, light gray), 2 mm (macrofauna exclusion, gray), and 6 mm (no soil fauna exclusion, white) in each forest type.

Fig. 4. Litter decomposability (% litter mass remaining of litter mixtures incubated in a common garden) in invaded (gray circles and dotted line) and non-invaded forest (gray squares and solid line). Squares and circles represent mean values of litter mass remaining over time ($\pm$ SE, n = 5) in each forest type.

Figures

Fig.1.

Fig.2.

Fig.3.

Fig.4.

Tables

Table 1. Results of generalized linear mixed models (using likelihood ratio test) examining the effects of forest type (invaded and non-invaded), mesh size of litterbags (0.01 mm; 2 mm and 6 mm) and time (30, 90 and 180 days) on litter meso- and macrofauna abundance. Site and time was included as a random effect.

	Response variables	DF	z	p
Litter fauna abundance	Forest type	1	7.10	<0.001
	Mesh size	2	6.57	<0.001
	Time	2	-6.12	<0.001
	Forest type × Mesh size	1	-3.33	<0.01
	Forest type × Time	2	-5.32	<0.001
	Forest type × Mesh size × Time	2	4.22	<0.001

Table 2. Results of generalized linear mixed model examining the effects of forest type (invaded and non-invaded), mesh size of litterbags (0.01, 2 and 6 mm) and time (30, 90 and 180 days), on leaf litter decomposition (% litter mass loss). Sites and time were included as a random effect.

	Response variables	D F	F	p
Litter mass loss (%)	Forest type	1	274.5	<0.001
	Mesh size	2	22.9	<0.001
	Time	2	1759.87	<0.001
	Forest type × Mesh size	2	5.5	0.052
	Forest type × Time	2	98.9	<0.001
	Mesh size × Time	4	7.9	<0.001
				1

Table 3. Soil parameters (mean ± SE, n=5) of invaded and non-invaded forests.

	Invaded forest	Non-invaded forest	p
Soil moisture (%)	30.5 ± 1.8	38.1 ± 1.8	0.02
Litter depth (cm)	1.2 ± 0.2	3.3 ± 0.2	<0.001

Soil pH	6.76 ± 0.1	6.19 ± 0.1	<0.01
SOM (%)	15.6 ± 0.6	17.5± 0.8	0.1
Soil N content (%)	0.7 ± 0.03	0.8 ± 0.04	0.14

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Appendices

Table A1. Total abundance of soil fauna collected in litterbags with 2 and 6 mm mesh size on invaded and non-invaded forest (n=5).

Taxa	invaded (2 mm)	non-invaded (2 mm)	invaded (6 mm)	non-invaded (6 mm)
Acari	908	1217	486	733
Aranae	0	0	1	6
Coleoptera	0	0	5	12
Collembola	408	681	154	523
Diptera	1	2	7	6
Gastropoda	2	2	0	0
Embiopoda	0	0	0	1
Haplotaenidae	22	15	37	16
Hemiptera	0	0	0	1
Hymenoptera	0	0	10	20
Isopoda	1	8	4	13
Psocoptera	19	18	8	28
Symphyla	0	4	1	0
Thysanoptera	1	5	0	12

Table A2. Pairwise contrasts between forest type (invaded and non-invaded), mesh size (0.01, 2 and 6 mm) and time (30, 90 and 180 days). SE: standard error. p-values in bold indicate significant differences.

Time	Contrast	Estimate	SE	p
30 days	non-invaded vs invaded	3.3	0.925	0.0062
90 days	non-invaded vs invaded	5.58	0.925	<.0001
180 days	non-invaded vs invaded	27.28	0.925	<.0001
30 days	0.01 vs 2 mm	-3.776	0.974	0.0047
30 days	0.01 vs 6 mm	-3.529	1.116	0.0476
30 days	2 vs 6 mm	-0.247	0.994	1
90 days	0.01 vs 2 mm	1.552	0.974	0.807
90 days	0.01 vs 6 mm	-4.839	1.116	0.0008
90 days	2 vs 6 mm	3.287	0.994	0.031
180 days	0.01 vs 2 mm	36.820	0.981	<.0001
180 days	0.01 vs 6 mm	-11.646	1.116	<.0001
180 days	2 vs 6 mm	6.274	0.994	<.0001

Table A3. Pairwise contrasts between forest type (invaded and non-invaded) and mesh size (0.01, 2 and 6 mm). SE: standard error. p-values in bold indicate significant differences.

Forest type	Contrast	Estimate	SE	p
invaded	0.01 v 0.2	-2.35	1.6	0.6822
invaded	0.01 v 0.6	-4.43	1.6	0.0668
invaded	0.2 v 0.6	2.08	1.6	0.7836
non-invaded	0.01 v 0.2	-4.41	1.6	0.0692
non-invaded	0.01 v 0.6	-12.06	1.6	<.0001
non-invaded	0.2 v 0.6	7.65	1.6	0.0001

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