

Changes in spider diversity through the growth cycle of pine plantations in the semi-deciduous Atlantic forest: The role of prey availability and abiotic conditions

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ABSTRACT

The replacement of native forests by tree plantations affects the diversity of biological communities, particularly in highly diverse tropical and subtropical ecosystems such as the semi-deciduous Atlantic forest. Previous studies in this ecosystem have focused on vertebrates, while only a few studies have been performed on the relationship between spiders and pine plantations. We aimed to estimate changes in spider richness and species composition over the course of a pine plantation forestry cycle of 15 years. We expected that the increase in environmental similarity (vegetation, prey availability) between native forest and tree plantations through the plantation growth cycle would promote its use by native spider species. We used six collection methods to characterize the spider assemblages and their potential prey in five replicates of native forest and pine plantations of three different ages representing the forest cycle (1–2, 5–6, 10–11 years old). Additionally, we described vegetation structure and recorded ground temperature and humidity during the sampling period. Analyses were carried out combining spiders from all sampling methods and independently on each vertical stratum. As expected, spider richness increased and the dissimilarity in relation to the native forest spider community decreased through the growth cycle of the pine plantation, associated with an increase in potential prey abundance and richness (but not vegetation structure). The response of spiders on each stratum showed interesting trends; opposite to the general pattern, in young plantations the ground strata exhibited a rich and distinctive spider assemblage while herbaceous strata showed similar diversity (richness and species composition) in all three plantation ages. Our results showed a rapid increase in spider richness in the first 6–7 years after plantation and a subsequent stabilization. Also, the proportion of native species in plantations increased from 6% in the first years to 34% and then remained constant until cutting age (11–12 years). Differences in species composition were mainly due to both differences in richness and species composition in young plantations, while in middle-aged and mature plantations it was mainly due to species replacement. The increase in prey abundance (and probably the increase in vegetation complexity and the decrease of extreme microclimatic conditions) through the plantation cycle increase the suitability for native forest species. However, a deeper understanding of the ecological and physiological requirements of spiders is necessary to improve the ability of tree plantations for native diversity.

1. Introduction

Globally, urban expansion and the replacement of native forest by agricultural and forestry intensive systems are the main causes of natural ecosystem and biodiversity loss (Miranda et al., 2016). In 2015, tree plantations represented only 7% of global forest area. However, in the coming decades, the area of tree plantations will increase as a consequence of the increasing demand for wood and timber products (United Nation's Food and Agriculture Organization, 2015). In general,

the replacement of natural forests by tree plantations affects the diversity (both the richness and the composition) of biological communities (Greene et al., 2016). However, the magnitude of these changes depends on factors acting at regional, landscape and local scale (Filloy et al., 2010; Zurita and Bellocq, 2012). At local scale, biological diversity in tree plantations and the suitability of these to support native biota depends on several aspects, including the planted tree species and density, stand age and silvicultural management (Brockerhoff et al., 2008; Fonseca et al., 2009).

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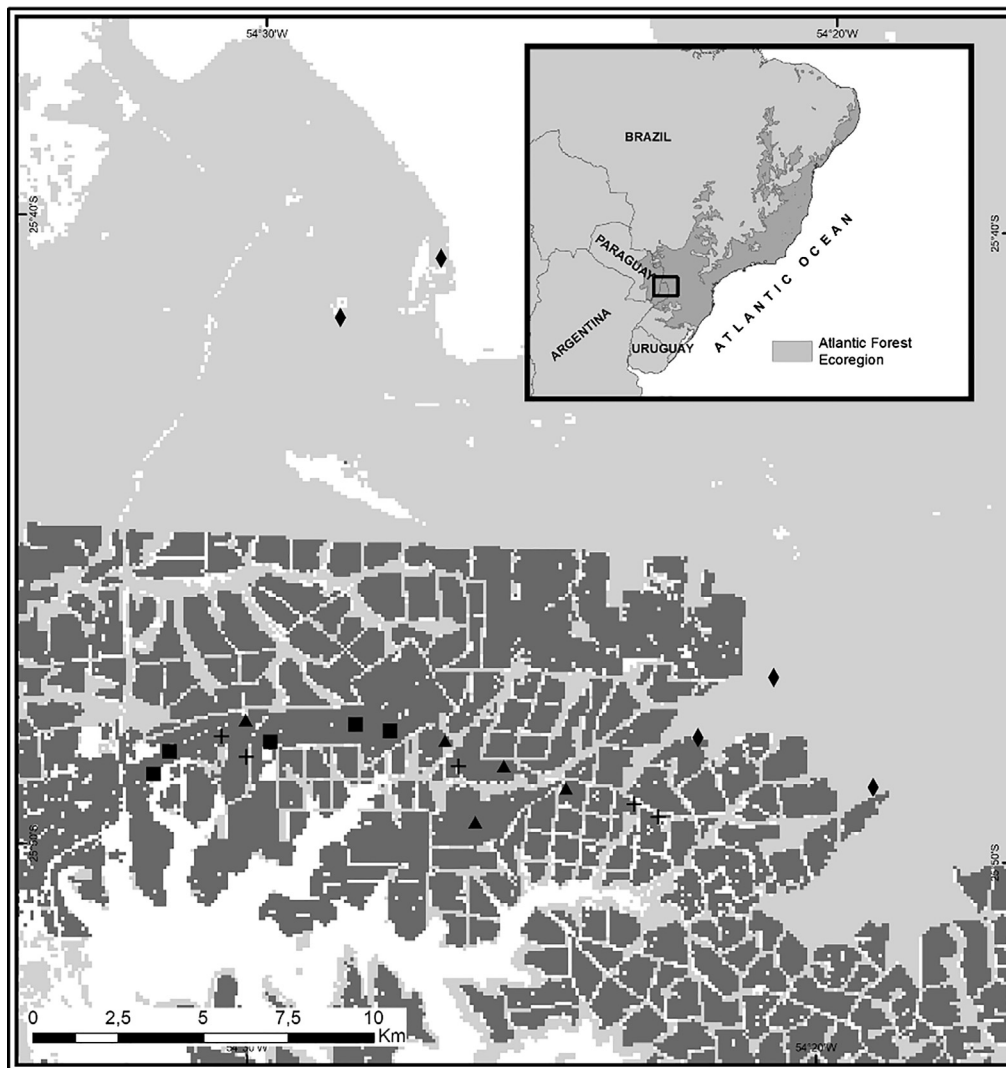


Fig. 1. Sampling sites in pine (*Pinus taeda*) plantations of three different ages (black), continuous native forest (light grey) and pine plantations (dark grey) in the semi-deciduous Atlantic forest of Argentina. Native forest (◆), mature plantation (▲), middle-aged plantation (■) and young plantation (+).

In the case of stand age, previous studies on birds, ground insects and spiders in tropical and subtropical forests showed a recovery of the native forest community (both richness and composition) through plantation growth; mature stands are used by a higher number of native forest species compared to young stands (Barbaro et al., 2005; Finch, 2005; Oxbrough et al., 2010, 2005; Berndt et al., 2008; Van Halder et al., 2008). This increase in the suitability of tree plantations for supporting native species is associated with the development and stabilization of forest biotic and abiotic conditions (Lo-Man-Hung et al., 2008; Ziesche and Roth, 2008), from the extreme simplified vegetation structure in young stands to a more complex multi-stratified vegetation in middle-aged and mature stands. Also extreme ground temperature in younger plantations decreases with stand age, becoming similar to native forest temperatures (Peyras et al. 2013). In the case of dung beetles, the lower ground temperature and humidity in mature plantations, which is similar to those of native forests, promotes the presence of native forest species (Peyras et al., 2013).

Spiders (Arachnida) are a globally mega diverse group, with almost 47,000 species described (WSC, 2017), recognized for their ecological role as generalist predators, mainly of arthropods (Roig-Juñent et al., 2014). The long-distance dispersal mechanisms of spiders (e.g., ballooning and cursorial activity) and the ecological amplitude of niche dimensions (e.g. diet, foraging strata, hunting strategies) allow them to inhabit almost all terrestrial ecosystems, including highly disturbed

habitats such as cities, agricultural areas and tree plantations (Nyffeler and Birkhofer, 2017; Pearce and Venier, 2006). Although some studies have compared the diversity of spiders in tree plantations and native forest (Gonzales, 2013; Samu et al., 2014), few have evaluated the response of spider assemblages at different vegetation strata to changes in biotic and abiotic variables caused by the replacement of the native forest.

The Atlantic forest of South America is one of the most biodiverse and threatened ecosystems in the world (1–8% of total global diversity). Currently less than 8% of the original cover survives and the remaining forest is highly fragmented (Ribeiro et al., 2009). The replacement of the native forest has been driven mainly by intensive productive systems such as agriculture, livestock and tree plantations (Lende, 2016). Previous studies on the effects of the replacement of the semi-deciduous Atlantic forest (the southern portion of the Atlantic forest) have focused on vertebrates (Cruz et al., 2014; Di Bitetti et al., 2006; Fonseca et al., 2009; Zurita et al., 2006) and some groups of arthropods (Baldissera et al., 2012; Peyras et al., 2013). According to Castanheira et al. (2016) and Rubio (2016), about 800 spider species have been recorded for the semi-deciduous Atlantic forest. However, little is known about the arachnid fauna of forest plantations adjoining the native forest and no studies have evaluated the temporal patterns of changes in diversity associated with the growth cycle of tree plantations.

The objectives of this study were (1) to describe changes in spider

species richness and composition of assemblages, particularly regarding those associated with the native forest community through a pine plantation cycle in the semi-deciduous Atlantic forest, and, (2) to associate changes in the abundance of potential prey availability and vegetation structure with spider diversity. We hypothesized that the increase in vegetation complexity and the abundance of potential prey through plantation growth will promote use by native forest species, increasing species richness and the similarity with the native forest spider assemblage.

2. Materials and methods

2.1. Study area

The study was performed in the semi-deciduous Atlantic forest of Argentina (25°48'6"S, 54° 22'14"W). Average annual precipitation reaches 2000 mm annually, without seasonality, with average temperature of 15°C in winter (June–August) and 25°C in summer (September–March) (Ligier et al., 1990). The canopy reaches 20–40 m and is composed of evergreen and deciduous tree species forming three to five strata with high abundance of vines. The understory is composed mainly of shrubs, bamboo and ferns (Campanello et al., 2011).

The landscape of the sampling area is composed of native forest in continuous areas (Iguazú National Park, Urugua-í Provincial Park and private reserves), forest fragments of variable size and adjacent pine plantations (*Pinus taeda*) of different ages, mainly for pulp production (Zurita and Bellocq, 2010) (Fig. 1).

2.2. Experimental design

Spiders were collected in December, January, February, and March of the spring-summer 2014–2015; the period of greatest spider activity in the Atlantic forest (Avalos et al., 2009, 2013; Rubio, 2016). Within the study area, we selected three different ages of *Pinus taeda* plantations: (1) young plantations (1–2 years old), (2) middle-aged plantations (6–7 years old) and (3) commercially mature plantations (11–12 years old). Ages were selected to represent a cycle during which the microclimatic conditions and the vertical vegetation structure change (Peyras et al., 2013). Five replicates, separated by a minimum distance of 500 m and with an average stand size of 27.1 ha (SD = 13.3; max = 68.9 ha; min = 10.5 ha), were selected for each age group (ESM Table A.1). Pine plantations in the study area are destined to cellulose pulp production, with an average density of 2 × 3 m between trees, without pruning or thinning, and a cycle of 12–13 years (Zaninovich et al., 2016).

In addition, five sites of continuous native forest were chosen including the Iguazu National Park and a private reserve (control sites). Native forest control sites were selected as representative of the original forest spider assemblage (before forest replacement) in the study area. According to the proposed hypothesis the suitability of tree plantation for native forest species increases with stand age. Consequently, the non-disturbed native forest spider community constitutes a reference community to explore these changes in both richness and composition through plantation growth. Both the Iguazu national Park and the private reserve are included in one of the largest remaining continuous areas of native Atlantic forest. In both areas, native forest exhibits a low level of disturbance (mainly because of selective logging in the past). Native stands had a basal area between 18 and 32 m² ha⁻¹, five arboreal strata and tree richness between 50 and 70 species ha⁻¹ (Chediack 2008; Zaninovich et al. 2017).

2.3. Sampling methods

Six collection methods were used to characterize the taxonomic diversity of spider assemblages and their potential prey diversity in the native forest and pine plantations. The methods were related to the

vegetation layers (ground, herbaceous, shrubs and low arboreal strata) used by different spider guilds (Dias et al., 2010; Azevedo et al., 2014). All sampling methods were performed twice in the four sampling months (eight sampling periods in total).

To characterize the diversity of ground spiders, we used pitfall traps and Winkler sacks. In each replicate, we installed five traps for each stand, 100 traps in total). Each trap separated by 50 m were operated for eight days each month. Pitfall traps were filled with propylene glycol (5% propylene glycol – 95% water) as preservative solution. In the case of Winkler sacks, we collected litter in two 1 × 1 m quadrats, and then sifted and deposited the litter in a closed bag for three days to collect spiders (two subsamples for each plantation age and control site, 40 samples in total).

To characterize spiders in the herbaceous strata, we used an entomological vacuum (G-VAC). In each sampling site, we randomly selected five sampling points separated by 10 m to maximize the sampling area (20 replicates, 100 sampling points in total). Vegetation 0 to 50 cm high in a 3 m ratio was aspirated for 1 min in each point (5 min per replica). The aspirated content was deposited in a hermetic bag of 20 × 20 cm filled 1/3 with alcohol 80% to fix the collected specimens.

To characterize spiders in the shrubs and low arboreal stratum, we performed minor and major beating on the vegetation. In the first case (minor beating), five shrubs 1.5 to 2 m high were selected; then, a 50 × 50 cm sheet was placed under the foliage to capture spiders and the vegetation was shaken for 15 continuous seconds, twice per shrub (30 s. per shrub in total). In the second method (major beating), five trees of 3–6 m high were selected; then, a 2 × 3 m sheet was placed under the canopy and the trees were shaken for two periods of 15 s (20 replicas, 100 sampling points). No beating was performed in young pine plantations due to the absence of this stratum (the maximum height of vegetation in young plantations did not exceed 50 cm). Finally, we performed nocturnal and diurnal hand collection to capture spider species usually not collected with the methods previously mentioned. For this purpose, two people carried out an *Ad Hoc* method for 20 min and captured all spiders accessible at any height (stratum).

All collected individuals were preserved in alcohol (80%), counted and identified as species or morphospecies by using specialist taxonomic guides (ESM B.1) and consultation with specialists from the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina. To quantify the potential prey availability, all non-spider arthropods captured by means of the pitfall traps, Winkler sacks and G-VAC vacuum cleaner were identified to order level. All specimens were deposited in the arachnological collection of the Instituto de Biología Subtropical (IBSI-Ara, G. Rubio), Misiones, Argentina.

To describe vegetation structure, two 10 × 10 plots (separated by 50 m) were established on each replicate (in both native forest and tree plantations). On each plot, an abundance-cover scale (0–100%) was used to estimate the cover of: grasses, brushwood, bare soil, ferns, litter, shrubs and herbaceous vegetation. Cover on each plot was averaged for each replicate. The temperature and relative humidity of the different environments were recorded with automatic temperature and relative humidity sensors (HOBO pro) during the sampling periods.

2.4. Statistical analyses

To explore forest age effects on the whole spider community, we analyze spiders collected across all strata for each stand. However, since species on each stratum may exhibit a differential response, we also explored changes in species richness and composition independently. In all cases (complete assemblage and on each stratum), the spider community of native forest (estimated from the native forest control sites) was used as a reference to test our hypothesis of change on species richness and composition.

To estimate sampling coverage and compare true alpha diversity (in the complete assemblage and on each stratum) we calculated diversity

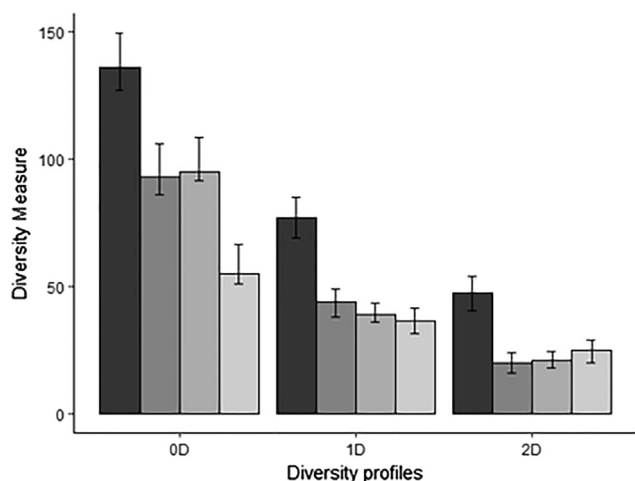


Fig. 2. Spider alpha diversity (all combined strata) in the native forest (black), mature pine plantation (dark grey), middle-aged pine plantation (grey) and young pine plantation (light grey) in the semi-deciduous Atlantic forest of Argentina; 0D (species richness), 1D (Exponential of Shannon index or evenness) and 2D (Inverse of Gini-Simpson index or dominance) with 95% confidence intervals.

orders 0D , 1D and 2D with a confidence interval of 95% by using iNEXT online (Chao and Jost, 2012) in pine plantations at different age (young, middle-aged, mature) and the native forest. 0D represents species richness. 1D considers not only the number but also the relative abundance of species and describes community evenness. 2D describes dominance in the community; lower values of 2D indicate higher dominance of a few numbers of species. Statistical differences in diversity were tested through confident intervals overlap (Jost and González-Oreja, 2012).

To explore changes in species composition between each age of pine plantations and the native forest, first we carried out a non-metric multidimensional scaling analysis (NMDS) using the abundance of species in each sampling site. To understand changes on species composition between native forest and tree plantations (either by species loss or gain and replacement), we first calculated the Jaccard index of dissimilarity (β_{cc}) between each plantation at different ages with the native forest (for the complete assemblage and for each stratum). Then, we decomposed the Jaccard index in two components: species replacement (β_{-3}) and species richness differences (β_{rich}), using the BAT package in R (Cardoso et al., 2015). We compared β_{-3} and β_{rich} between ages by using an ANOVA or Kruskal-Wallis with Tukey and post hoc comparisons, respectively.

To explore the impact of potential prey availability (abundance) and vegetation structure (abundance-cover) on the richness of spiders, we first performed two principal component analysis (PCA) based on the assemblage of potential prey orders (using the relative abundance) and vegetation structure, respectively. PCAs were performed to reduce the number of explanatory variables for both preys and vegetation using Vegan and APE package from R software. The scores from the first and second axes of PCAs, were used as explanatory variables, and richness of spiders as the response variable in a GLM analysis. The model assumed a Poisson distribution and the parameters were tested through homoscedasticity and normality plots (ESM Table A.6). The model was performed using Agricolae package from R. Since vegetation structure and the availability of potential prey were estimated at the ground and understory strata, only spiders collected on these strata were considered on the GLM analysis.

3. Results

Microclimatic conditions changed through the plantation cycle; the average temperature was similar in middle-aged, mature plantations

and the native forest, but higher in young stands (23.3 °C, SD:0.3; 23.6 °C, DS:0.3; 23.5 °C, DS: 0.2; and 26.9 °C, DS:0.1 respectively). The maximum temperatures increased from native forest to young stands (33.5–41.2 °C, respectively, with 34.7 °C in mature and 38.3 °C in middle-aged stands) while the minimum temperature remained constant between 14 and 16 °C in all habitats. As well as temperature, average humidity was similar in native forest and middle-aged and mature plantations and lower in young stand (90.6%, 89.5%, 92.9% and 76.2%, respectively).

3.1. Patterns of alpha diversity

We collected 5441 individuals belonging to 246 species, of which 1759 adults were identified to species or morpho-species level. About 55.2% (136 out of the 246 species) were found in the native forest, 38.6% (95) in middle-aged plantations, 37.8% (93) in mature plantations and 22.3% (55) in young plantations. Native forest shared 34% of species with mature plantations, 33% with middle-aged plantations and 6% with young plantations. The most abundant species in mature and middle-aged plantations was *Miagrammopes guttatus* (Mello-Leitão, 1937), *Aillutticus nitens* (Galiano, 1987) in young plantations, and *Mangora msp2* in the native forest. Sampling coverage was over 85% in all habitats; therefore, we considered the sampling to be representative based on previous studies for the Atlantic forest (Argañaraz et al., 2017) (ESM Table A.2).

Regarding diversity at the assemblage level (grouping all strata), the native forest exhibited the highest richness (0D), whereas young plantations showed the lowest number of species; middle-aged and mature plantations showed a similar and intermediate number of species (Fig. 2). Evenness (1D) was higher in the native forest and similar in all plantations, while dominance (2D) was higher and similar in all pine plantations than in the native forest. Overall, results of alpha diversity showed lower richness and greater dominance of common species in pine plantations than in the native forest being middle-aged and mature plantations intermediate situations (Fig. 2).

The analysis of alpha diversity (tested through confidence intervals overlap) on each stratum showed that patterns of richness, evenness and dominance in all plantations and native forest vary among strata. At the ground stratum, the richness of species was similar in all plantations ages and higher in native forest. In this stratum, evenness was higher and dominance was lower in native forest and mature plantation compared to middle and young stand (Fig. 3a). At the herbaceous stratum, richness, evenness and dominance were similar among plantations and the native forest (Fig. 3b). In the understory stratum, species richness was higher on native forest, followed by middle-aged plantations and mature plantations, with the lowest richness in young plantation (Fig. 3c), while evenness and dominance were similar in all tree plantation ages. Finally, in the low arboreal stratum, richness and evenness were higher and dominance was lower in native forest compared to tree plantations (Fig. 3d).

3.2. Changes in species composition

The NMDS analysis for the complete assemblage (all combined strata) based on species abundance grouped the 20 stands into three clearly differentiated groups. The native forest formed a cluster separated from young plantations and from middle-aged and mature plantations; middle-aged and mature plantations formed two overlapping groups (Stress: 0.07; Fig. 4a). The NMDS analysis based on independent stratum showed different patterns of arrangement depending on the stratum. At the ground stratum, young plantations formed a separate cluster while native forest, middle-aged and mature plantations formed a single group (Stress: 0.16; Fig. 4b). On the herbaceous and low arboreal strata native forest formed a separate cluster from tree plantations whereas middle-aged, mature and young stands (in the case of the herbaceous stratum) formed a single group (Stress: 0.10, 0.13,

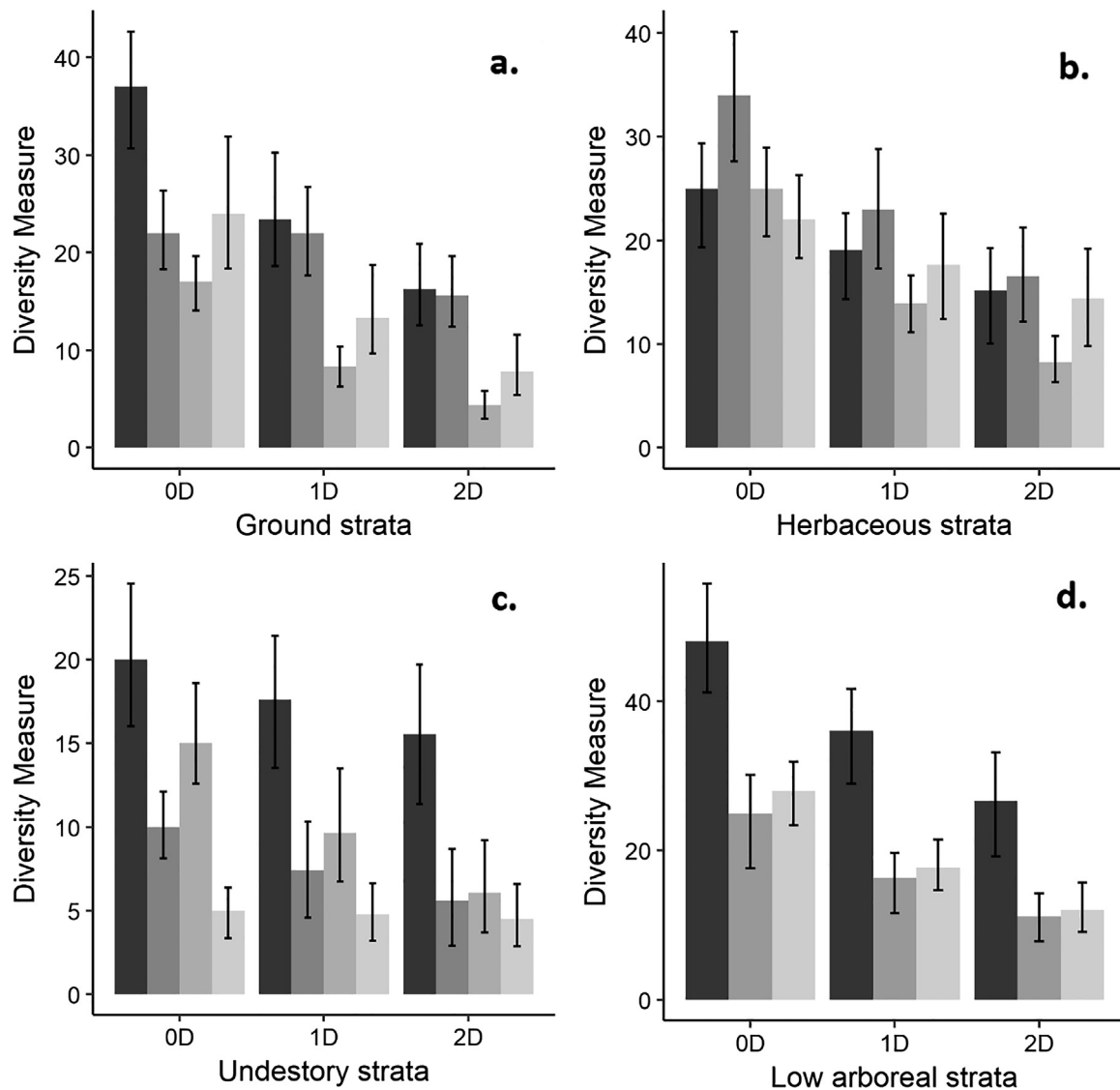


Fig. 3. Spider alpha diversity per stratum in native forest (black), mature pine plantation (dark grey), middle-aged pine plantation (grey) and young pine plantation (light grey) in the semi-deciduous Atlantic forest of Argentina. Ground stratum (a), herbaceous stratum (b), understory stratum (c) and low arboreal stratum (d). ⁰D (species richness), ¹D (Exponential of Shannon index) and ²D (Inverse of Gini-Simpson index) with 95% of confident intervals.

respectively) (Fig. 4c, d).

The results of the dissimilarity (β_{cc}) analysis were consistent with those of the NMDS (Fig. 4a). Combining all strata, young plantations exhibited the highest dissimilarity in species composition in relation to the native forest. This was a consequence of both species replacement (β_{-3}) and differences on species richness (β_{rich}). In contrast, differences between mature and middle-aged plantations and the native forest were mainly a consequence of species replacement (richness was similar) (Fig. 5, ESM Table A.3). At the ground stratum, differences between young plantations and native forest were mainly a consequence of species replacement while both differences on species richness and species replacement explained the dissimilarity between native forest and middle-aged and mature plantations. At the herbaceous stratum differences between young plantations and native forest was for both species replacement and differences on species richness; referring to middle-aged and mature plantations differences on species composition in herbaceous and low arboreal strata were explained by species replacement, mainly (ESM Table A.4).

3.3. Vegetation structure, prey availability and spider richness

The first two axis of the PCA based on potential prey assemblage explained 35% of the variation in prey abundance (23% and 12% respectively). The first axis in the analysis was positively associated to native forest stand, mature and middle-aged plantations and most prey orders (ESM. A.5) while the second axis were negative associated to young plantations stands and Hymenoptera (Formicidae) and Isopoda orders. In the case of vegetation, the first two axis explained 65% (34% and 31%) of the variation on vegetation structure. In this case, the first axis was positively associated to mature plantation and the cover of litter, grasses and herbaceous vegetation. Native forest and middle-aged plantation were negatively associated to shrubs, brushwood and ferns. The second axis was positively associated to young plantation and bare soil.

The GLM performed with the richness of spiders at the ground and herbaceous strata and the first two axes of the prey and vegetation cover PCAs showed that only the first axis of prey had a positive and significant effect ($z = 4.75$, $df = 13$, $P < 0.01$) while the second axis of prey ($z = 0.39$, $P = 0.69$, $df = 13$) and both vegetation PCA axes had no influence ($z = -0.10$, $p = 0.92$, $df = 13$ and $z = 0.58$, $p = 0.55$,

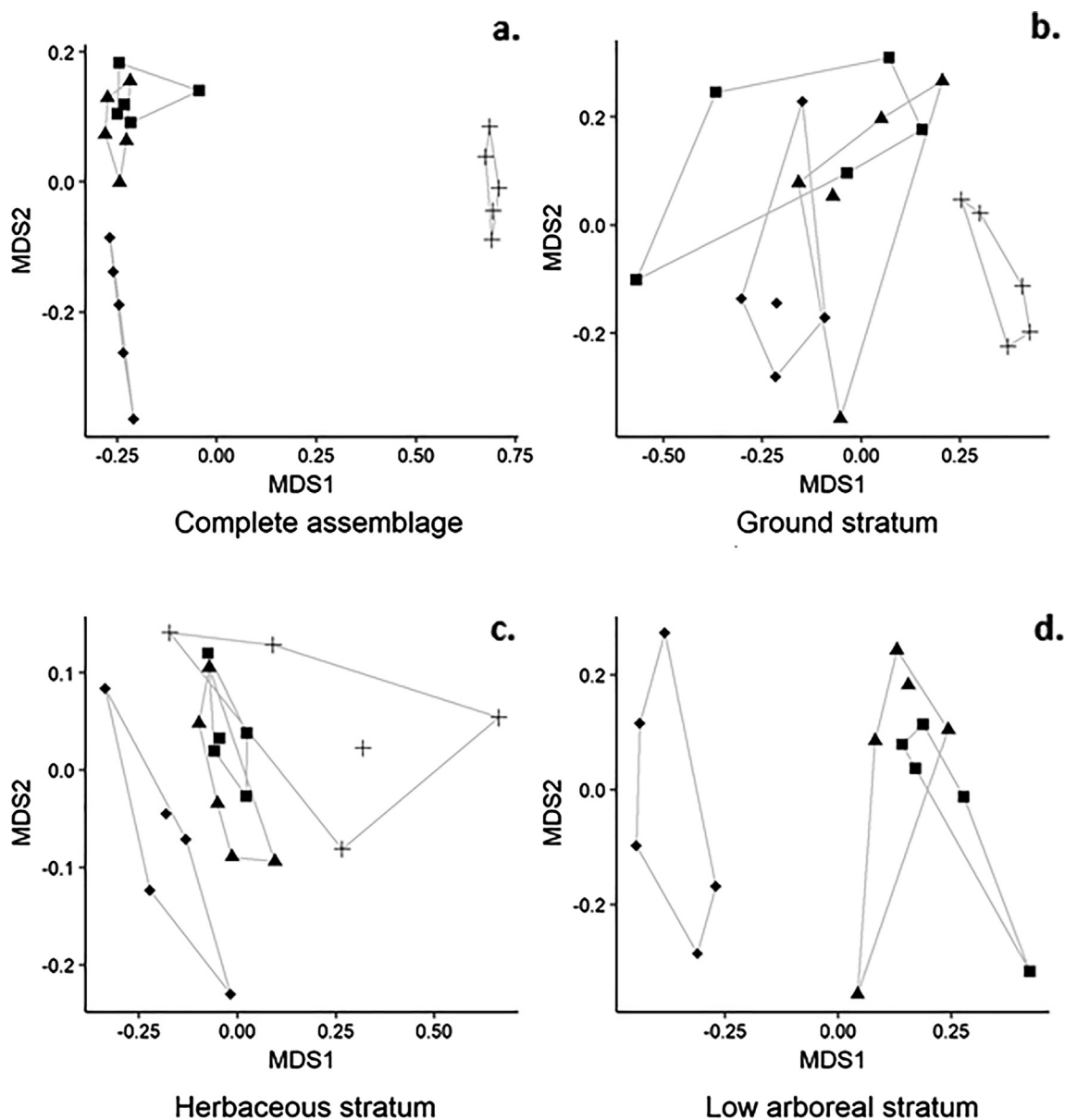


Fig. 4. Non-metric Multidimensional Scaling (NMDS) analysis of the composition of spider assemblages in native forest and pine plantations of different ages grouping all strata (a) and on each independent stratum (b-d) in the semi-deciduous Atlantic forest of Argentina. Native forest (♦), mature plantation (▲), middle-aged plantation (■) and young plantation (+).

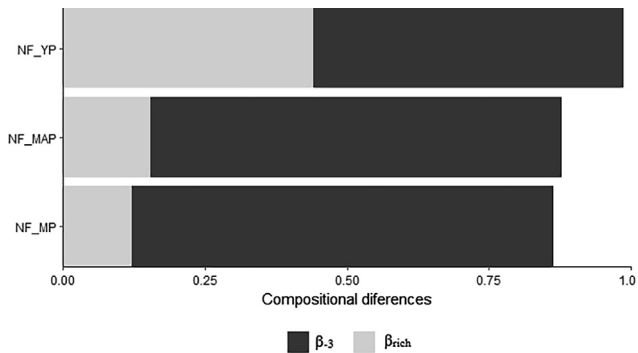


Fig. 5. Dissimilarity (β_{cc} index) in species composition and component of species replacement (β_3) and species richness differences (β_{rich}) between the native forest and tree plantations of different ages in the semi-deciduous Atlantic forest of Argentina. Native forest (NF), mature plantations (MP), middle-aged plantations (MAP) and young plantations (YP).

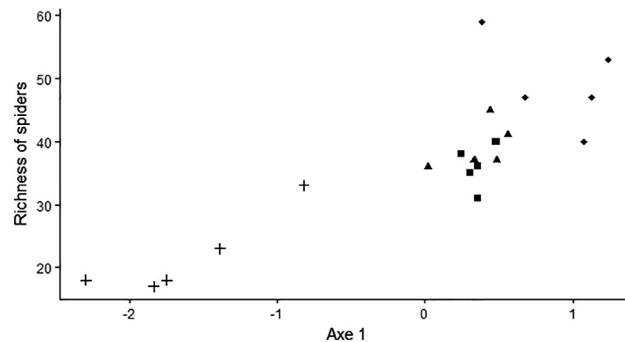


Fig. 6. Relation between richness of spider at the ground and herbaceous strata and first axis of a PCA analysis based on the abundance of potential prey orders in the native forest (diamond), mature plantations (triangles), middle-aged plantations (squares) and young plantations (crosses) in the semi-deciduous Atlantic forest of Argentina.

df = 13, respectively) (ESM. A.6) (Fig. 6).

4. Discussion

As hypothesized, there was an increase in the use of tree plantations by native forest spiders with plantation age, which results in higher richness and similarity of species composition between native forests and older plantations compared to young stands. While general results support our hypothesis, we also observed that total richness and the percentage of native forest species (33–34% of native forest species) inhabiting plantations was similar between middle-aged plantations (six years old) and those close to the cutting age (11 years old). This means, the aptitude of tree plantations for native Atlantic forest spiders showed a marked increase from planting to canopy closure (approximately 6–7 years old) and remained constant until the end of the cycle. Canopy closure is one of the main determinants of spider diversity (both richness and composition) in forests through the regulation of soil microclimate, allowing the development of understory vegetation and the diversity and abundance of potential preys (Finch, 2005; Lange et al., 2011; Oxbrough et al., 2010, 2005; Ziesche and Roth, 2008).

While the general pattern of change in species richness and composition through the growth cycle was consistent with previous studies (Oxbrough et al., 2005, 2010), the response of spiders at each stratum differed. The total number of species was the lowest in young plantations, but at ground and herbaceous strata young plantations showed a distinctive and richer spider assemblage. Unlike native forest and older stands, young plantations are characterized by bare soil – herbaceous vegetation composed mainly of grasses and extreme values of temperature and humidity – which could explain the distinctive spider assemblages in these strata. In contrast, the scarce understory development and the absence of an arboreal stratum explains the low total number of species recorded on this habitat. On the other hand, the canopy closure in middle-age and mature plantations (Harms et al., 2000) reduce extreme microclimatic conditions, thus allowing the maintenance and development of understory and arboreal vegetation (Calviño-Cancela et al., 2012). These conditions promote an increase in richness and abundance of spiders using those strata, particularly native forest species. High plantation density and the absence of thinning and pruning in these plantations promote a fast canopy closure, explaining the similarities in environmental conditions and probably the composition of spiders (Schultz, 1997).

Previous studies have shown that spider diversity is strongly dependent on prey richness and abundance, and vegetation structure (Hendrickx et al., 2007; Samu et al., 2014; Raub et al., 2015). Carvalho et al. (2015) proposed that the availability of prey is a direct factor for the richness and abundance of spiders, while abiotic changes (temperature, precipitation, humidity, etc.) have an indirect influence through the regulation of prey diversity and abundance; therefore, we could infer that the regulation of abiotic conditions through the plantation cycle facilitates the increase in richness and abundance of prey and consequently promotes the use of tree plantations by native spiders. Vegetation structure is also a key component to spiders inhabiting understory and arboreal strata, particularly for orb web, space web, hunter and ambusher guilds (Lopes Rodrigues and Mendonça, 2012). In our study, we found a strong relation between the abundance of certain prey orders (Collembola, Diptera, Acari, Blatodea and Orthoptera) with the richness of ground and herbaceous spiders; however, we were not able to find a relation with vegetation structure. Vegetation structure is particularly important for web-building spiders, however we only considered species captured on the ground and herbaceous strata (mainly ground hunters and runners species) since prey abundance was only estimated for those strata. Vegetation structure would probably be a major determinant for understory an arboreal species.

As previously mentioned, the development of a vertical structure of vegetation and the decrease on extreme temperatures in middle-ages and mature plantations allows the colonization by native forest spiders

requiring these structures. Although we found a strong positive relationship between potential prey richness and spider richness at the ground and herbaceous strata, we cannot exclude the possibility that underlying factors (biotic and abiotic) are affecting all arthropods in a similar way, leading to the observed association. It is also important to note that the richness and abundance of orders of potential prey is a rough estimator that may not reflect the actual availability of spider prey due to differences in preference among species diets, although spiders are considered generalist predators (Birkhofer et al., 2007).

Our results show that the aptitude of tree plantations for native spiders increases with plantation age in the Atlantic forest of Argentina, probably because of the establishment of conditions more similar to native forest, including microclimate, prey availability and vegetation structure. However, the proportion of native spider species (33–34%) was relatively low and constant in plantations older than 6 years, suggesting that there are other factors limiting the use of tree plantations in the semi-deciduous Atlantic forest of Argentina. High plantation density, short cycles and the use of agrochemicals limit the development of vegetation structure and the abundance of different arthropod groups (Hanson et al., 2017). In contrast, habitat diversification within plantations increases the abundance of prey and reduces the intra-specific spider competition and cannibalism among spiders by increasing ecological niches and decreasing the rate of inter-species encounters (Michalko et al., 2017). Also, the number of native species in tree plantations may increase through plantation cycle because of differential rate of colonization (dispersal abilities).

Spiders are the main arthropod predators in disturbed and natural ecosystems, consuming nearly 24 million tons of arthropods per year in agroecosystems and an estimated of 697 million tons of arthropods per year in natural habitats (Nyffeler and Birkhofer, 2017). Consequently, changes in spider richness and abundance throughout the growth cycle of plantations could have important effects on the development and control of forestry pests (such as Hemiptera, Coleoptera, Hymenoptera, Lepidoptera and Orthoptera) due to changes in the proportion (numerical or biomass) of spiders over prey (Sunderland and Samu, 2000).

More profound mechanisms limiting the use of anthropogenic habitats by native spider fauna will require specific studies on the ecological requirements (diet) and physiological tolerance to the environmental conditions of different species. Particularly, a large proportion of native species were not present in tree plantations in the Atlantic forest of Argentina, irrespectively of plantation age. A better understanding of these mechanisms and specific requirements would allow the design of forest plantations with a greater ability to support native fauna

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.03.025>.

References

Avalos, G., Bar, M.E., Oscherov, E.B., González, A., 2013. Diversidad de Araneae en

- cultivos de *Citrus sinensis* (Rutaceae) de la Provincia de Corrientes, Argentina. *Revista de Biología Tropical* 61 (3), 1243–1260.
- Avalos, G., Damborsky, M.P., Bar, M.E., Oscherov, E.B., Porcel, E., 2009. Composición de la fauna de Araneae (Arachnida) de la Reserva provincial Iberá, Corrientes, Argentina. *Revista de Biología Tropical* 57, 339–351.
- Azevedo, G.H.F., Faleiro, B.T., Magalhães, I.L.F., Benedetti, A.R., Ubirajara, O., Pena-Barbosa, J.P., Santos, M.T., Vilela, P.F., De Maria, M., Santos, A.J., 2014. Effectiveness of sampling methods and further sampling for accessing spider diversity: a case study in a Brazilian Atlantic rainforest fragment. *Insect Conserv. Divers.* 381–391. <http://dx.doi.org/10.1111/icad.12061>.
- Argañaraz, C.I., Rubio, G.D., Gleiser, R.M., 2017. Jumping spider (Araneae:Salticidae) diversity in the understory of the Argentinian Atlantic Forest. *Ecología*. <http://dx.doi.org/10.15446/caldasia.v39n1.60527>.
- Baldissera, R., Rodrigues, E.N.L., Hartz, S.M., 2012. Metacommunity composition of web-spiders in a fragmented neotropical forest: relative importance of environmental and spatial effects. *PLoS One* 7. <http://dx.doi.org/10.1371/journal.pone.0048099>.
- Barbaro, L., Pontcharrard, L., Vettillard, F., Guyon, D., Jactel, H., 2005. Comparative responses of bird, carabid, and spider assemblages to stand and landscape diversity in maritime pine plantation forests. *Ecoscience* 12, 110–121. <http://dx.doi.org/10.2980/11195-6860-12-1-110.1>.
- Berndt, L.A., Brockerhoff, E.G., Jactel, H., 2008. Relevance of exotic pine plantations as a surrogate habitat for ground beetles (Carabidae) where native forest is rare. *Biodivers. Conserv.* 17, 1171–1185. <http://dx.doi.org/10.1007/s10531-008-9379-3>.
- Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? *Biodivers. Conserv.* 17, 925–951. <http://dx.doi.org/10.1007/s10531-008-9380-x>.
- Birkhofer, K., Scheu, S., Wise, D.H., 2007. Small-scale spatial pattern of web-building spiders (Araneae) in Alfalfa: relationship to disturbance from cutting, prey availability, and intraguild interactions. *Environ. Entomol.* 36(4), 1, 801–810. <https://doi.org/10.1093/ee/36.4.801>.
- Calviño-Cancela, M., Rubido-Bará, M., van Etten, E.J.B., 2012. Do eucalypt plantations provide habitat for native forest biodiversity? *For. Ecol. Manage.* 270, 153–162. <http://dx.doi.org/10.1016/j.foreco.2012.01.019>.
- Campanello, P.I., Genoveva Gatti, M., Montti, L., Villagra, M., Goldstein, G., 2011. Ser o no ser tolerante a la sombra: Economía de agua y carbono en especies arbóreas del bosque atlántico (Misiones, Argentina). *Ecol. Austral* 21, 285–300.
- Cardoso, P., Rigal, F., Carvalho, J.C., 2015. BAT – Biodiversity Assessment Tools, an R package for themeasurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods Ecol. Evol.* 6, 232–236. <http://dx.doi.org/10.1111/2041-210X.12310>.
- Carvalho, L., Sebastian, N., Araujo, H.F.P., Dias, S.C., Venticinque, E., Brescovit, A.D., Vasconcellos, A., 2015. Climatic variables do not directly predict spider richness and abundance in semiarid Caatinga vegetation, Brazil. *Environ. Entomol.* 44 (1), 54–63. <http://dx.doi.org/10.1093/ee/evu003>.
- Castanheira, P., Pérez-González, A., Baptista, R., 2016. Spider diversity (Arachnida: Araneae) in Atlantic Forest areas at Pedra Branca State Park, Rio de Janeiro, Brazil. *Biodivers. Data* 4, e7055. <http://doi.org/10.3897/BDJ.4.e7055>.
- Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93 (12), 2533–2547.
- Chediack, S., 2008. Efecto de la explotación forestal sobre la estructura, diversidad y composición florística de los palmitales de la Selva Atlántica en Misiones, Argentina. *Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744)* 56 (2), 721–738.
- Cruz, P., Paviolo, A., Bó, R.F., J.J., Thompson, Di Bitetti, M.S., 2014. Daily activity patterns and habitat use of the lowland tapir (*Tapirus terrestris*) in the Atlantic Forest. *Mamm. Biol.* 79, 376–383. <http://dx.doi.org/10.1016/j.mambio.2014.06.003>.
- Di Bitetti, M.S., Paviolo, A., De Angelo, C., 2006. Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. *J. Zool.* 270, 153–163. <http://dx.doi.org/10.1111/j.1469-7998.2006.00102.x>.
- Dias, S.C., Carvalho, L.S., Bonaldo, A.B., Brescovit, A.D., 2010. Refining the establishment of guilds in Neotropical spiders (Arachnida: Araneae). *J. Nat. History* 44 (3–4), 219–239. <http://dx.doi.org/10.1080/00222930903383503>.
- Filloj, J., Zurita, G.A., Corbelli, J.M., Bellocc, M.I., 2010. On the similarity among bird communities: testing the influence of distance and land use. *Acta Oecol.* 36, 333–338. <http://dx.doi.org/10.1016/j.actao.2010.02.007>.
- Finch, O.D., 2005. Evaluation of mature conifer plantations as secondary habitat for epigeic forest arthropods (Coleoptera: Carabidae; Araneae). *For. Ecol. Manage.* 204, 21–34. <http://dx.doi.org/10.1016/j.foreco.2004.07.071>.
- Fonseca, C.R., Ganade, G., Baldissera, R., Becker, C.G., Boelter, C.R., Brescovit, A.D., Campos, L.M., Fleck, T., Fonseca, V.S., Hartz, S.M., Joner, F., Käffer, M.I., Leal-Zanchet, A.M., Marcelli, M.P., Mesquita, A.S., Mondin, C.A., Paz, C.P., Petry, M.V., Piovensan, F.N., Putzke, J., Stranz, A., Vergara, M., Vieira, E.M., 2009. Towards an ecologically-sustainable forestry in the Atlantic Forest. *Biol. Conserv.* 142, 1209–1219. <http://dx.doi.org/10.1016/j.biocon.2009.02.017>.
- Greene, R.E., Iglay, R.B., Evans, K.O., Miller, D.A., Wigley, T.B., Riffell, S.K., 2016. A meta-analysis of biodiversity responses to management of southeastern pine forests—opportunities for open pine conservation. *For. Ecol. Manage.* 360, 30–39. <http://dx.doi.org/10.1016/j.foreco.2015.10.007>.
- Gonzales C., 2013. Comparación de la araneofauna de un cultivo de pino (*Pinus taeda*) con la matriz de campo natural. Tesis de Maestría.
- Harms, W.R., Whitesell, C.D., DeBell, D.S., 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. *Forest Ecol. Manage.* 126, 13–24.
- Hanson, H.I., Birkhofer, K., Smith, H.G., Palmu, E., Hedlund, K., 2017. Agricultural land use affects abundance and dispersal tendency of predatory arthropods. *Basic Appl. Ecol.* 18, 40–49. <http://dx.doi.org/10.1016/j.baec.2016.10.004>.
- Hendrickx, F., Maelfait, J.P., Van Wingerden, W., Schweiger, O., Speelmanns, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Herzog, F., Liira, J., Roubalova, M., Vandomme, V., Bugter, R., 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *J. Appl. Ecol.* 44, 340–351. <http://dx.doi.org/10.1111/j.1365-2664.2006.01270.x>.
- Jost, L., González-Oreja, J.A., 2012. Midiendo la diversidad biológica: mas allá del índice de Shannon. *Acta Zoologica Lilloana* 56 (1–2), 3–14.
- Lange, M., Weisser, W.W., Gossner, M.M., Kowalski, E., Türke, M., Joner, F., Fonseca, C.R., 2011. The impact of forest management on litter-dwelling invertebrates: a subtropical-temperate contrast. *Biodivers. Conserv.* 20, 2133–2147. <http://dx.doi.org/10.1007/s10531-011-0078-0>.
- Lende, S.G., 2016. Industria forestal y acumulación por desposesión en la Argentina: el caso de Alto Paraná S. A. en la Provincia de Misiones. *Revista Geografía Agraria*, 11(22), 38–68.
- Ligier, H.D., Matteio, H.R., Polo, H.L., Rosso, J.R., 1990. Provincia de Misiones. In: Atlas de suelos de la República Argentina, Tomo II. Centro de Investigaciones de Recursos Naturales, INTA, Secretaría de Agricultura, Ganadería y Pesca. Buenos Aires, Argentina, pp. 111–154.
- Michalko, R., Petraková, L., Sentenská, L., Pekár, S., 2017. The effect of increased habitat complexity and density-dependent non-consumptive interference on pest suppression by winter-active spiders. *Agric. Ecosyst. Environ.* 242, 26–33. <http://dx.doi.org/10.1016/j.agee.2017.03.025>.
- Miranda, A., Altamirano, A., Cayuela, L., Lara, A., González, M., 2016. Native forest loss in the Chilean biodiversity hotspot: revealing the evidence. *Reg. Environ. Change* 1–13. <http://dx.doi.org/10.1007/s10113-016-1010-7>.
- Lo-Man-Hung, N.F., Gardner, T.A., Ribeiro-Júnior, M.A., Barlow, J., Bonaldo, A.B., 2008. The value of primary, secondary, and plantation forests for Neotropical epigeic arachnids. *Am. Arachnol. Soc.* 21, 775–787. <http://dx.doi.org/10.1111/j.1523-1739.2007.00659.x>.
- Lopes Rodrigues, E.N., Mendonça, M.S., 2012. Spiders guilds in the tree-shrub strata of riparian forests in southern Brazil. *J. Arachnol.* 40, 39–47.
- Nyffeler, M., Birkhofer, K., 2017. An estimated 400–800 million tons of prey are annually killed by the global spider community. *Sci. Nat.* 104, 30. <http://dx.doi.org/10.1007/s00114-017-1440-1>.
- Oxbrough, A., Irwin, S., Kelly, T.C., O'Halloran, J., 2010. Ground-dwelling invertebrates in reforested conifer plantations. *For. Ecol. Manage.* 259, 2111–2121. <http://dx.doi.org/10.1016/j.foreco.2010.02.023>.
- Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Smith, G.F., 2005. Structural indicators of spider communities across the forest plantation cycle. *For. Ecol. Manage.* 212, 171–183. <http://dx.doi.org/10.1016/j.foreco.2005.03.040>.
- Pearce, J.L., Venier, L.A., 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review. *Ecol. Indic.* 6, 780–793. <http://dx.doi.org/10.1016/j.ecolind.2005.03.005>.
- Peyras, M., Vespa, N.I., Bellocc, M.I., Zurita, G.A., 2013. Quantifying edge effects: the role of habitat contrast and species specialization. *J. Insect Conserv.* 17, 807–820. <http://dx.doi.org/10.1007/s10841-013-9563-y>.
- Raub, Florian, Höfer, H., Scheuermann, L., Miranda de Brites, R., Brandl, R., 2015. Conserving landscape structure—conclusions from partitioning of spider diversity in southern Atlantic Forest of Brazil. *Studies on Neotropical Fauna and Environment*. <http://doi.org/10.1080/01650521.2015.1071959>.
- Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biol. Conserv.* 142, 1141–1153. <http://dx.doi.org/10.1016/j.biocon.2009.02.021>.
- Roig-Juñent, S., Claps, L.E., Morrone, J.J., 2014. Biodiversidad de Artrópodos Argentinos volumen 3. Editorial INSUE – UNT, San Miguel de Tucumán, Argentina.
- Rubio, G.D., 2016. Using a jumping spider fauna inventory (Araneae: Salticidae) as an indicator of their taxonomic diversity in Misiones, Argentina. *Rev. Biol. Trop. (Int. J. Trop. Biol.)* 64 (2), 875–883.
- Samu, F., Lengyel, G., Szita, É., Bidló, A., Ódor, P., Va Szita, É., Dor, P., 2014. The effect of forest stand characteristics on spider diversity and species composition in deciduous-coniferous mixed forests. *J. Arachnol.* 42, 135–141. <http://dx.doi.org/10.1636/CP13-75.1>.
- Schultz, R.P., 1997. Loblolly pine. The Ecology And culture of Loblolly Pine (*Pinus taeda* L.). Agricultural handbook. Washington, DC 20402-9328.
- Sunderland, K., Samu, F., 2000. Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. *Entomologia Experimentalis et Applicata* 95, 1–13*****.
- United Nation's Food and Agriculture Organization, 2015. Global Forest Resources Assessment 2015: How are the world's forests changing? Nations, Food and Agriculture Organization of the United Rome 2015. <http://dx.doi.org/10.1002/2014GB005021>.
- Van Halder, I., Barbaro, L., Corcket, E., Jactel, H., 2008. Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations. *Biodivers. Conserv.* 17, 1149–1169. <http://dx.doi.org/10.1007/s10531-007-9264-5>.
- WSC, 2017. World Spider Catalog. Natural History Museum Bern, online at <http://wsc.nmbe.ch>, version 18.5, (accessed on {6 September}). <http://doi.org/10.24436/2>.
- Zaninovich, S.C., Fontana, J.L., Gatti, M.G., 2016. Atlantic Forest replacement by non-native tree plantations: Comparing aboveground necromass between native forest and pine plantation ecosystems. *For. Ecol. Manage.* 363, 39–46. <http://dx.doi.org/10.1016/j.foreco.2015.12.022>.
- Zaninovich, S.C., Montti, L.F., Alvarez, M.F., Gatti, M.G., 2017. Replacing trees by bamboos: Changes from canopy to soil organic carbon storage. *For. Ecol. Manage.* <http://dx.doi.org/10.1016/j.foreco.2017.05.047> 0378-1127/.
- Ziesche, T.M., 2008. Roth, M., 2008. Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: what makes the difference, tree species

- or microhabitat? *Forest Ecol. Manage.* 255, 738–752.
- Zurita, G.A., Bellocq, M.I., 2012. Bird assemblages in anthropogenic habitats: identifying a suitability gradient for native species in the Atlantic forest. *Biotropica* 44, 412–419. <http://dx.doi.org/10.1111/j.1744-7429.2011.00821.x>.
- Zurita, G.A., Bellocq, M.I., 2010. Spatial patterns of bird community similarity: Bird responses to landscape composition and configuration in the Atlantic forest. *Landsc. Ecol.* 25, 147–158. <http://dx.doi.org/10.1007/s10980-009-9410-4>.
- Zurita, G.A., Rey, N., Varela, D.M., Villagra, M., Bellocq, M.I., 2006. Conversion of the Atlantic Forest into native and exotic tree plantations: effects on bird communities from the local and regional perspectives. *For. Ecol. Manage.* 235, 164–173. <http://dx.doi.org/10.1016/j.foreco.2006.08.009>.