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Policy analysis

Past and present effects of habitat amount and fragmentation *per se* on plant species richness, composition and traits in a deforestation hotspot

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ABSTRACT

Worldwide, human activities are rapidly changing land cover and its spatial configuration. While it is widely acknowledged that habitat loss is a major cause of biodiversity loss, there is less agreement on how biodiversity responds to changes in habitat configuration. We assessed the effects of forest amount and forest fragmentation *per se* (the number of patches for a given forest amount, an aspect of configuration) on woody species richness, composition, and traits in the Dry Chaco forest, a global deforestation hotspot. We sampled woody plants in 24 forest sites varying in forest amount and fragmentation *per se* in the surrounding landscapes. Using Generalized Linear Modeling we tested whether a model with just forest amount was at least as able to predict species richness as a model with either patch size or isolation or the combination of both. We also tested whether forest amount and fragmentation *per se* influenced species richness, composition, and the density of four species traits. Finally, we compared these responses to forest amount and fragmentation *per se* measured in the past (2009) *vs.* in the present (2017) to look for time-lagged responses. We found that: 1) in support of the habitat amount hypothesis, species richness was more strongly related to forest amount than to the size and/or isolation of the forest patch containing the sample plot; 2) the positive effect of forest amount on species richness was more important than the effect of fragmentation *per se* (also positive); 3) fragmentation *per se* changed species composition such that plots in landscapes with more fragmented forest had species with smaller leaves and seeds, and higher wood density; and 4) species richness showed a time-lagged response to forest amount but not to forest fragmentation *per se*. Our results suggest that preservation of native Dry Chaco forest should be prioritized regardless of its fragmentation level, for conserving woody plant species diversity.

1. Introduction

Worldwide, human activities are rapidly changing land cover and land-use patterns with negative consequences for biodiversity and ecosystem functioning (Foley et al., 2005; Haddad et al., 2015; Newbold et al., 2015). However, despite much research on this topic, there are still knowledge gaps regarding the effects of landscape structure (*e.g.* the amount of natural habitat and its spatial arrangement) on biodiversity and its functioning (Marull et al., 2019). This is particularly noteworthy in subtropical dry forests, which have recently experienced agricultural expansion causing some of the highest deforestation rates in the world (Hansen et al., 2013) and have not received much attention regarding

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the effects of forest loss and fragmentation on biodiversity.

While it is widely acknowledged that habitat loss is a major cause of biodiversity loss (Newbold et al., 2015), there is less agreement on how biodiversity responds to changes in habitat configuration (Fahrig et al., 2019; Fletcher et al., 2018; Miller-Rushing et al., 2019). Indeed, an interesting debate is currently taking place about the effects on biodiversity of 'fragmentation *per se*', *i.e.*, the effect of breaking apart of habitat into multiple patches, for a given habitat amount. While it is usually stated that fragmentation has negative effects on biodiversity (Debinski and Holt, 2000; Fletcher et al., 2018; Haddad et al., 2015), most studies that assessed biodiversity responses to fragmentation have confounded the breaking apart of habitat with habitat loss effects (Fahrig, 2019). Furthermore, studies assessing fragmentation effects on species abundance, occurrence, and richness while controlling for habitat amount (fragmentation *per se*) usually find no effect and, if any, a positive effect (Fahrig, 2017). In addition, some models indicate that negative effects of habitat fragmentation *per se* will occur only at low levels of habitat amount (Fahrig, 1998).

Fahrig (2013) proposed a simple view of the relationship between habitat amount and species richness at a sample plot (*i.e.* species density), called the 'habitat amount hypothesis' (HAH). The HAH implies a null expectation of no effect of habitat fragmentation *per se* on species richness in a sample plot. According to the HAH, the number of species at a sample plot depends on the amount of habitat surrounding that plot, within its 'local landscape', *i.e.*, the area of influence of the surrounding landscape on the plot. Essentially, the more habitat there is within the local landscape, the more individuals it contains. For a given species abundance distribution, this implies more species in the local species pool available to colonize the sample plot. The HAH suggests that observed effects of patch size and isolation on species richness are simply due to correlations (positive and negative, respectively) between these variables and habitat amount in the local landscape. Thus, the HAH predicts that a model containing just the amount of habitat in the local landscape can predict species richness at least as well as a model containing either the size or the isolation of the patch containing the sample plot, or both (Fahrig, 2013). While the HAH does not make direct predictions about the effect of habitat fragmentation *per se* on species richness in a sample plot, it indirectly implies that there would be no effect. This is because, for a given amount of habitat in the local landscape of the sample plot, varying the size and/or isolation of the patch containing the sample plot requires varying the configuration of the habitat in the local landscape. If, consistent with the HAH, the size and isolation of the patch containing the sample plot do not affect species richness in the plot once habitat amount is controlled for, this would imply that the configuration of habitat in the local landscape does not affect species richness in the plot. As habitat fragmentation *per se* is an aspect of habitat configuration, this would also imply no effect of fragmentation *per se*. Thus, the HAH provides theoretical underpinning for an expected lack of effect of habitat fragmentation *per se* on species richness in sample plots. If, in contrast, an effect of fragmentation *per se* is observed, we can infer that processes are at play that go beyond a simple relationship between habitat amount and the species pool available for colonizing the sample plot (potential processes are reviewed in Fahrig et al., 2022). While the most comprehensive test to date supported the HAH (Watling et al., 2020), some individual studies have not supported it (Evju and Sverdrup-Thygeson, 2016; With and Payne, 2021).

In addition to their effects on species richness, habitat amount and fragmentation *per se* may also affect community composition. And, if an effect on species composition causes shifts in the distributions of different species traits in the community, this could also affect ecosystem processes (Díaz and Cabido, 2001). A variety of ecosystem processes such as tree mortality, carbon storage, primary productivity, seedling survival and ability to tolerate disturbances have stronger links with species composition than with species richness (Díaz and Cabido, 2001; Greenwood et al., 2017; Westoby et al., 1996).

Here we study the effects of forest amount and fragmentation *per se* on forest woody plant species richness, species composition, and distribution of four species traits in forest sample plots. For forest amount, we predict an increase in species richness with the forest amount due to the sample area effect as described above: a larger total area of habitat will contain more individuals and, for a given abundance distribution, this will imply more species available to colonize the forest plot (Fahrig, 2013). As forest amount decreases, we predict a change in composition such that rare species will be more prone to disappear (Hubbell et al., 2008). Also, we predict that populations of tree species whose seed dispersal depends on rare and small-ranging animal species will decrease (Staude et al., 2020).

While we expect little effect of forest fragmentation *per se* on forest plant species richness (see above), we might see effects of forest fragmentation *per se* on species composition and associated shifts in the distributions of traits (Zambrano et al., 2019). Fragmentation *per se* increases the amount of forest edge in the landscape (Saunders et al., 1991), which should favour some species over others due to changes in microclimate, energy flows and biological interactions (Liu et al., 2019). For example, a hotter environment at edges may favour species having small leaves and therefore less water loss (Zambrano et al., 2019). Thus, in landscapes with more fragmented habitat - many small patches and more forest edge -, there will be more immigration of edge-related species into forest interior plots. Tree species on forest edges often have lower wood density, are shorter and have lower specific leaf area than forest-interior trees (Rodrigues et al., 2016; Wright et al., 2013). Edge habitats also favour wind-pollinated pioneer plant species with small seeds (Liu et al., 2019) and a capacity to tolerate disturbance and water stress (Lasky et al., 2013). Extrapolating these local edge effects to a landscape scale, we predict that these traits will be more common in landscapes with higher forest fragmentation *per se* (and thus more forest edge), regardless of the location of the sample plot(s). The prevalence of some traits over others might then affect ecosystem functions such as primary productivity, food resources and carbon storage (Hertzog et al., 2019), so it is important to understand how fragmentation *per se* affects these traits.

In addition, effects of habitat amount and fragmentation *per se* on species richness and community composition could be delayed, as the effects of many processes such as pollination, dispersal, population establishment, species interactions, and genetic drift play out over long time periods (Brooks et al., 1999; Hanski and Ovaskainen, 2002; Metzger et al., 2009; Tilman et al., 1994). The possibility of delayed responses to habitat amount and fragmentation *per se* is especially relevant in rapidly changing agricultural frontiers such as those in subtropical forest ecoregions (Graesser et al., 2015; Semper-Pascual et al., 2018). Given this recent forest loss, we expect that the remaining forests still retain many species that will eventually disappear. This might make the current species richness and composition more similar to past landscape structure than to present landscape structure. For example, we predict that plots in landscapes with higher forest amount in the past will have higher current plant species richness than those with lower forest amount in the past, for the same current amount of forest.

The Argentine Dry Chaco is a suitable region to test these predictions because: i) it is an endangered, understudied, and low-protected biome (Hansen et al., 2013; Hoekstra et al., 2004), and ii) agricultural expansion is driving rapid loss and fragmentation of the remaining forest (Gasparri and Grau, 2009; Piquer-Rodríguez et al., 2015; Carranza et al., 2015; Velasco-Aceves et al., 2021). The Argentine Dry Chaco forest has experienced one of the highest rates of deforestation in the world (Hansen et al., 2013); the latest published estimate is 5 million hectares of forest lost between 2000 and 2019 (de la Sancha et al., 2021; Baumann et al., 2022). Forest loss and fragmentation were initially related to road construction for logging, and some small-scale agriculture (Piquer-Rodríguez et al., 2015). In recent decades, these processes increased due to large-scale agricultural expansion. This expansion began in areas with better soils and near towns (Gasparri and Grau, 2009) and then spread to nearby areas (Piquer-Rodríguez et al., 2018; Volante et al., 2016). This has resulted in different landscape configurations, with varying sizes and distributions of forest fragments within the agricultural matrix. Indeed, in different parts of the region, the same amount of forest can be distributed in a few large patches or in several small ones, allowing an analysis of the influence of forest fragmentation independently of forest amount. Although Dry Chaco landscapes are experiencing a huge transformation due to agricultural expansion, evidence for the effects of this transformation on vegetation diversity and species composition is lacking. Furthermore, the little existing evidence (Cagnolo et al., 2006; Torrella et al., 2013, 2015) has not evaluated the effects of fragmentation *per se* (as in Fahrig, 2003).

We tested the habitat amount hypothesis and we assessed the effects of forest amount *vs* forest fragmentation *per se*, measured as the number of patches for a given forest amount, on woody species richness and composition, and four plant traits in vegetation plots in the Dry Chaco forests. We asked: (1) Does the woody plant community in Dry Chaco support the habitat amount hypothesis? (2) What are the effects of forest amount and fragmentation *per se* on species richness, species composition, and plant traits including wood density, height at maturity, leaf area, and seed dry mass? (3) Is there a time-lag response of species richness and plant traits to changing forest amount and fragmentation *per se*?

2. Methods

2.1. Study site description

The study was conducted in the NE of the province of Santiago del Estero, Argentina (Fig. 1). This area is located in the Dry Chaco region, and the Semi-arid Chaco sub-region (Morello et al., 2012; Oyarzabal et al., 2018). Here the climate is characterized by wet summers and dry winters, with large variability over years. The precipitation is around 750–800 mm while the mean annual temperature is 27.7 °C (Torres Bruchmann, 1981). The annual potential evapotranspiration is between 900 and 1000 mm and its monthly values generally exceed precipitation, particularly between May and October (Houspanossian et al., 2016).

The forests of the Dry Chaco are xerophytic and semideciduous. The mature forest is characterized by an upper stratum formed by the red quebracho (*Schinopsis lorentzii* (Griseb.) Engl.) and the white quebracho (*Aspidosperma quebracho-blanco* Schtdl.), exceeding 20 m height. Other important species in these forests are shorter and include the mistol (*Ziziphus mistol* Griseb.), the palo cruz (*Tabebuia nodosa* (Griseb.) Griseb.) and many species of the *Prosopis*, *Senegalia* and *Vachellia* genera, some of which have value for forestry and livestock raising (Torrella and Adámoli, 2006).

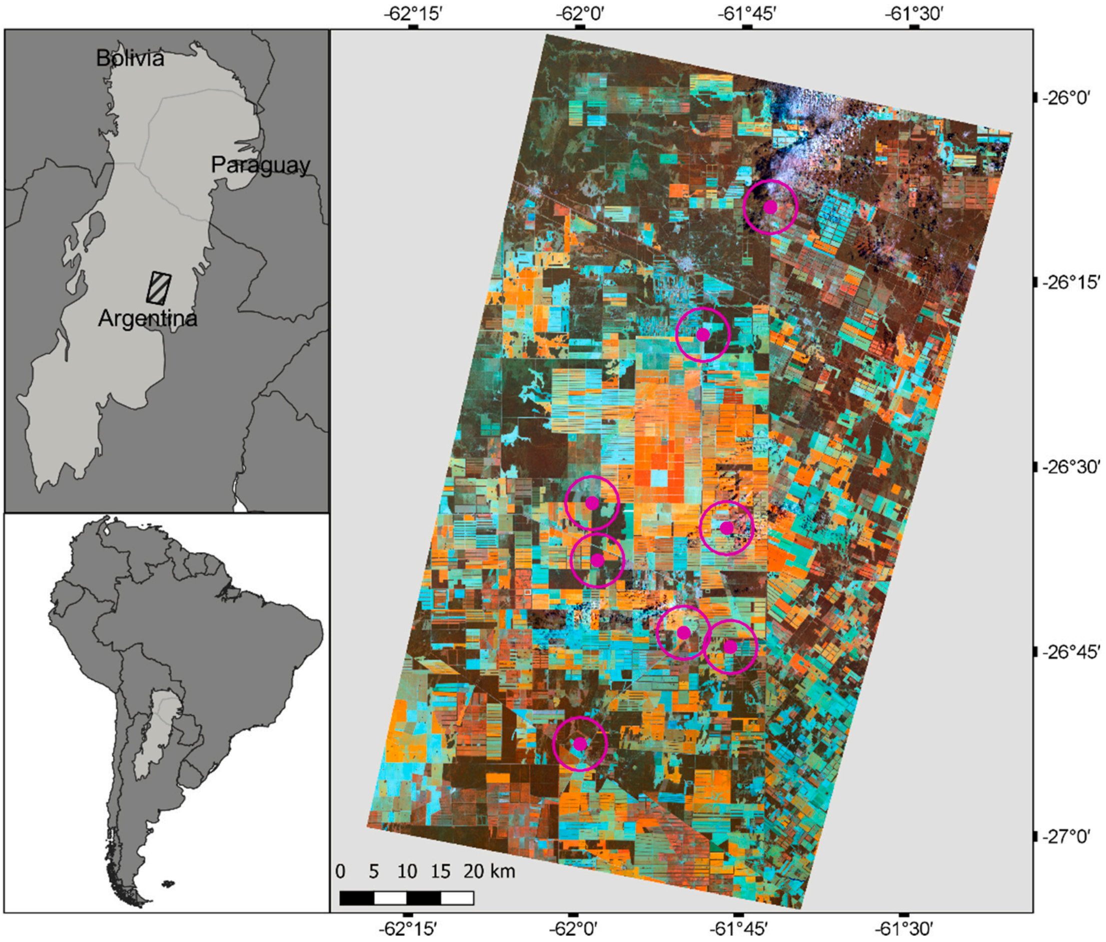

Fig. 1. Study area corresponding to a portion of the Dry Chaco Ecoregion in the northeast of Santiago del Estero Province, Argentina. Pink points indicate the locations where vegetation surveys were conducted (one point in the centre of each 3-km-radius landscape). Remaining forest (dark green) is surrounded by pastures or agricultural fields with high photosynthetic rate (reddish colours) or bare soil or recently sown agricultural fields (blue colours). The inset in the top left shows the location of the Dry Chaco Forests Ecoregion (light grey) in South-America (inset at the bottom left). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Data gathering

We identified the forest cover by classifying a mosaic of two Landsat 5 and Landsat 8 images from March and April 2017 and 2009 (LC08 and LC05, Path 229 / Row 78 and Path 228 / Row 78) through a *Linear Spectral Unmixing* algorithm using CLASlite 3.2 (Asner, 2009). We used these dates because in 2009 there was a deforestation peak, and therefore the changes in habitat amount and fragmentation were the highest; our field sampling took place in 2017. This algorithm decomposes each pixel of the Landsat mosaic into three constituent components, Photosynthetic Vegetation (PV), Non-Photosynthetic Vegetation (NPV) and Bare Soil (BS) from the comparison of their spectral signals with a spectral library of PV, NPV and BS built from field data (Asner, 2009). The resulting classification had the proportion of each pixel occupied by the components (PV, NPV and BS) which together reach 100 % of the pixel coverage. We considered a pixel with >70 % of PV and <20 % of BS as forest and the remaining pixels as non-forest (Camba Sans et al., 2021). To eliminate some pixels belonging to agricultural plots that met the proposed thresholds, we masked the resulting map with an actual version of the deforestation database for the study region elaborated by Vallejos et al. (2015).

On the classified image of 2017, we located the landholdings where we could get access and conduct fieldwork and established a circular area of 4 km radius around their central points (5000 ha). Within each circular area, we quantified the proportion of the landscape occupied by forests (habitat amount) and the number of forest patches (fragmentation *per se*). Subsequently, we selected the circular areas where the ranges for both metrics were maximized. In this way, there were four types of landscapes, each of them representing one of the following situations: landscapes with a high amount of forest distributed in a few large patches (Af), landscapes with low amount of forest distributed in a few large patches (af), landscapes with a high amount of forest distributed in many small patches (AF), and landscapes with low amount of forest distributed in many small patches (aF) (Fig. 2). We selected two landscapes within each type, making a total of eight sampled landscapes. Although we categorized the landscapes for site selection purposes, Habitat amount and Fragmentation '*per se*' were analyzed as continuous variables, not categorical variables. We used Fragstats v. 4.2.1. for calculating the patch and landscape metrics (McGarigal and Marks, 1995).

Within each landscape, in July 2017 we surveyed woody vegetation in 2–4 plots (24 plots total) separated by a minimum distance of 600 m. Plots were always within forest patches at a fixed distance of 200 m from forest edge. We used plots of 50 m × 10 m (500 m^2) for identifying and counting trees with a diameter at breast height (DBH) >10 cm and plots of 50 m × 2 m (100 m^2) for the rest of the woody vegetation (trees and shrubs <10 cm DBH). We measured the DBH of all trees that exceeded 10 cm.

2.3. Data analysis

2.3.1. Testing the habitat amount hypothesis

For testing the habitat amount hypothesis, we followed the approach of Fahrig (2013). This requires one to (i) empirically identify the size of the local landscape associated with each plot, by assessing the distance from the sample plots within which forest amount has the strongest effect on species richness, (ii) assess whether, at this spatial extent, there was sufficient independence between forest amount and the size and isolation of the patches where the plots were located to evaluate their relative effects, and (iii) compare the effects of forest amount to the effects of patch size and isolation on species richness in the sample plots, *i.e.* species density. Note the habitat amount hypothesis does not make any predictions about the overall magnitude of the habitat amount effect. It just predicts that its effect is stronger than the effects of patch size and patch isolation.

For the first step above, we estimated forest amount within various distances, from 1 to 8 km, of each plot, and calculated the correlation between forest amount at each spatial extent and species richness at the

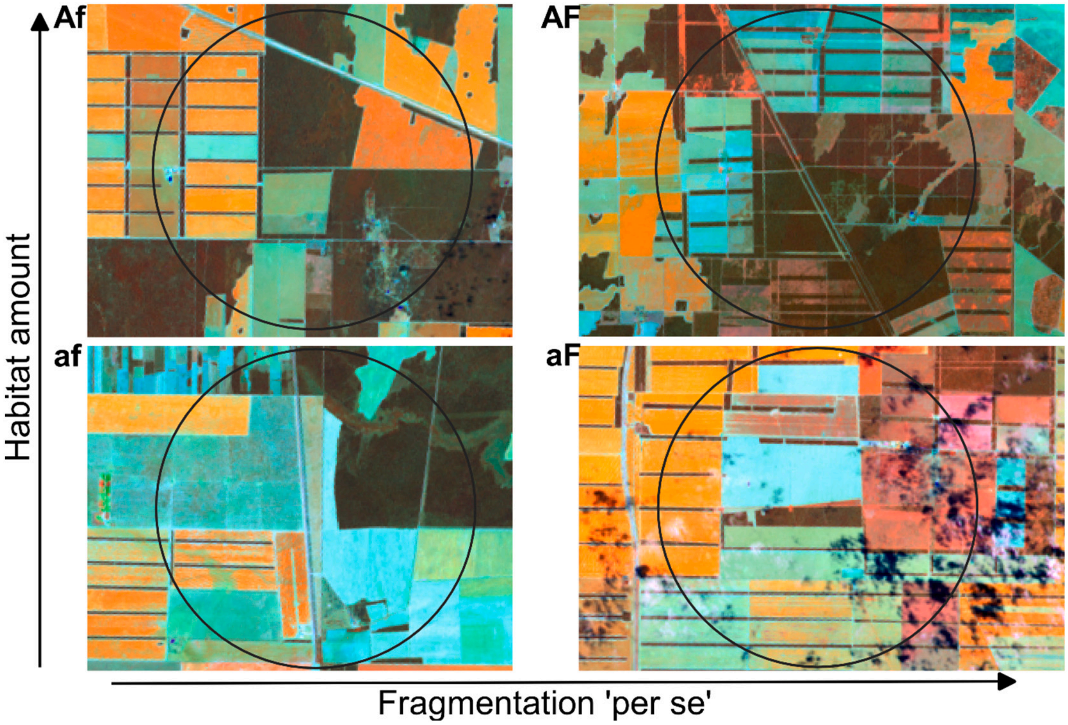

Fig. 2. Examples of the four landscape types selected *a priori* in this study. Each image has high (Af, AF) or low (af, aF) amount of remaining forest (dark green), distributed in a few large patches (Af, af) or several small patches (AF, aF), surrounded by pastures or agricultural fields with high photosynthetic rate (reddish colours) or bare soil or recently sown agricultural fields (blue colours). Two landscapes were selected within each type. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sample plots. The strongest correlation occurred for forest amount measured within 3 km of sampling plots (Appendix 1). For all analyses we therefore measured forest amount ("HAB") and fragmentation as the number of forest patches ("FRAG") in circular areas within 3 km of the sample plots. Thus, while for site selection (Section 2.2) we measured forest amount and fragmentation *per se* within each of eight 4-km radius landscapes, for data analysis we had 24 local landscapes of 3-km radius each, one for each sample plot (Appendix 2).

For the second step, we explored the Pearson correlation between HAB and the area of the patch containing the sample plot ("AREA"), and between HAB and the shortest distance (edge-to-edge) from the patch containing the sample plot to the next nearest patch ("DIST"). Both correlations were low (HAB-AREA, $r = 0.34$; HAB-DIST, $r = -0.11$), confirming the suitability of the sites selected to test the habitat amount hypothesis.

Finally, we used Generalized Linear Models to test the habitat amount hypothesis, *i.e.* whether the fit of a model of species richness in sample plots on only the predictor HAB was at least as good as a model on either AREA or DIST, or the combination of both. For this we compared the R^2 values of the four models (Smith et al., 2009).

2.3.2. *Assessing the effects of forest amount and fragmentation per se on species richness and composition*

We assessed the floristic composition of each plot by Detrended Correspondence Analysis (DCA), calculating the Bray-Curtis similarity index (Hill and Gauch, 1980) on the plots × species frequency matrix [24 × 25]. Regarding plant traits, for each species we gathered data on leaf area (data available for 18 species), wood density (available for 19 species) and seed dry mass (available for 6 species) from the TRY database at www.try-db.org/TryWeb/Data.php (Appendix 4). To calculate trait densities when these values were not available for all species, we did not consider these missing values. There were not enough data of maximum height at maturity in the TRY database, so we used plant growth form (tree or shrub) as an approximation for maximum height, assuming trees are taller than shrubs. We assigned a value of 1 to trees and 0.5 to shrubs and multiplied these values by the variable "Plant Growth Form Consensus" from the TRY dataset (DataID 6544) compiled by Engemann et al. (2016). These authors developed a decision framework to assign each species to a single "consensus growth form", which is the number of sources agreeing on the classification divided by the total number of sources with growth form information on the species. We used these traits to interpret DCA axes using Pearson correlations.

We used Generalized Linear Models to test for effects of HAB and FRAG on species richness, species composition and plant traits. Response variables were species richness, the logarithm of the coordinates of the DCA axes for each plot (species composition), and the logarithm of the density of plant traits in each transect. This last variable was calculated by multiplying the number of individuals of each species in each transect by the trait value of each species. We used a Poisson distribution for species richness models after checking for overdispersion. Note that we did not include patch metrics AREA and DIST in these models, because we were not testing the habitat amount hypothesis here.

2.3.3. *Assessing time-lag responses of species richness and composition to past landscape configuration*

To test for delayed responses to forest loss and fragmentation, we fit the above models to HAB and FRAG separately for 2009 and 2017. We considered that delayed responses to forest loss and fragmentation occurred if the AIC of the model using HAB and FRAG from 2009 was more than two units lower than the AIC of the model using HAB and FRAG from 2017 (Anderson and Burnham, 2004; Zuur et al., 2009). In all models, the predictor variables were standardized and the validity of the statistical assumptions was assessed through residual distribution analysis. We used the packages vegan (Oksanen et al., 2022), FD (Laliberté et al., 2022) and lme4 (Bates et al., 2015) in the software R for the above-mentioned analyses.

3. Results

3.1. *Testing the habitat amount hypothesis*

Consistent with the habitat amount hypothesis, the model of species richness that contained only HAB had a better fit (higher R^2) than the models with only AREA or only DIST, or both AREA and DIST (Table 1). These results support the habitat amount hypothesis for woody plants in dry Chaco forests.

3.2. *Effects of forest amount and fragmentation per se on species richness, composition and plant traits*

The correlation between forest amount and fragmentation *per se* (number of patches) within 3 km of the sample sites was −0.21 in 2017 and 0.28 in 2009 (Appendix 3). Consistent with the results from the test of the HAH above, the coefficient for the effect of fragmentation *per se* on species richness was very close to zero. The effect of forest amount was larger than the effect of fragmentation *per se*, but still small, which is consistent with the low R^2 value in Table 1 (Fig. 3A, Appendix 5). The coefficients were positive for both forest amount and fragmentation *per se*, indicating higher species richness in plots surrounded by a larger amount of forest divided into many small patches.

The first two axes of the Detrended Correspondence Analysis together explained 42 % of the variation among plots in plant composition (Fig. 4; Appendix 6). In contrast to the results for species richness, the effect of forest fragmentation *per se* on species composition was stronger than the effect of forest amount (Fig. 3A). This is seen in Fig. 4 where the sampling plots belonging to AF and aF (forest distributed in many patches: open symbols in Fig. 4) were located mainly in the upper half of either axis on the ordination plot. In contrast, the sampling plots of landscapes with high or low amount of forest (HAB) were more homogeneously distributed in the ordination plot, suggesting a weaker effect of forest amount on species composition.

The effects of HAB and FRAG on species composition were reflected in shifts in some species traits (Fig. 3, Appendix 5). Forest amount favoured tree species with higher wood density and higher leaf area. Forest fragmentation *per se* favoured tree species with higher wood density, smaller leaves and lower seed dry mass.

3.3. *Time-lag responses*

The comparison of standardized coefficients for models using predictors measured in 2009 *vs.* in 2017 suggested some lag effects of HAB (Fig. 3, Appendix 5). Most obvious was the stronger positive effect (difference of two AIC units between models) of HAB on species richness when HAB was measured in 2009 than in 2017. The same was true for the effect of HAB on wood density. The effect of HAB on species

Table 1
Results of the linear models relating plant species richness (log R) to forest amount (HAB) and patch size (AREA) and isolation (DIST). HAB is the amount of forest within 3 km of a sample plot ($n = 24$), AREA is the area of the forest patch containing a sample plot, and DIST is the distance from the edge of the patch containing a sample plot to the edge of the nearest forest patch, all measured in 2017.

	Std Estimate	SE	AIC	R2
Null model			118.730	0.000
HAB	0.038	0.058	120.330	0.040
AREA	−0.010	0.058	120.730	0.002
DIST	0.001	0.058	120.760	0.000
AREA + DIST	−0.012 0.005	0.063 0.062	122.720	0.018

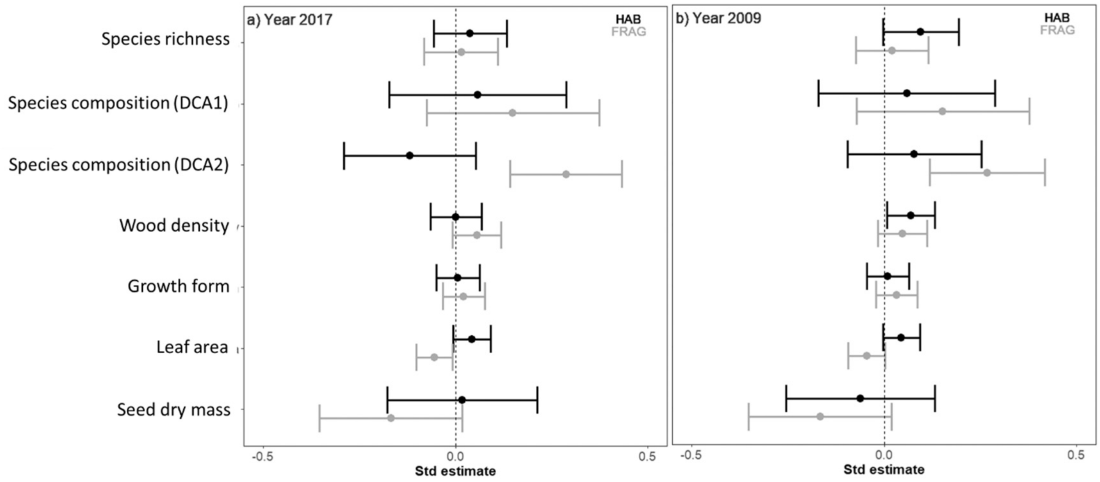

Fig. 3. Standardized estimates and confidence intervals of the relationships between plant species richness, species composition, and density of four plant traits *vs.* forest amount (HAB, black) and fragmentation *per se* (FRAG, grey) measured in 2017 (left panel) and in 2009 (right panel). HAB and FRAG were measured within 3 km of forest-interior plant sampling plots (n = 24).

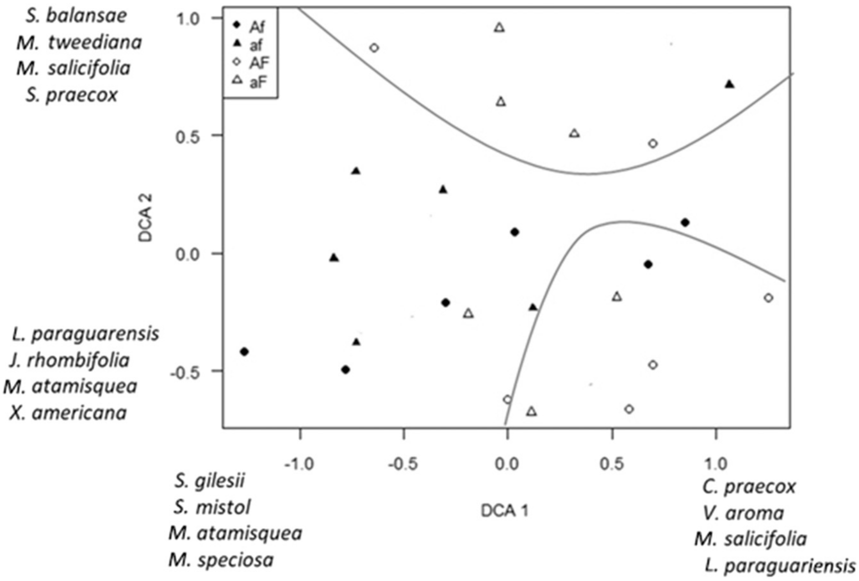

Fig. 4. Detrended Correspondence Analysis biplot of the 24 plots × 25 species matrix. Different colours refer to the degree of forest fragmentation *per se*, FRAG, measured as the number of forest patches within 3 km of the sampling plot (black, a few patches; white, many patches). Different symbols refer to the amount of forest within 3 km of the sample plots, HAB (circles, high forest amount; triangles, low forest amount). The four species with the highest positive and negative scores on both axes are shown.

composition was negative when HAB was measured in 2017 but positive when it was measured in 2009 (Fig. 3: DCA2). Finally, the effect of HAB on seed mass was neutral when HAB was measured in 2017 but negative when it was measured in 2009. For other responses and predictors, including all responses to FRAG, the standardized coefficients were similar whether the predictor was measured in 2009 or 2017 (Fig. 3, Appendix 5).

4. Discussion

4.1. Species richness

Our results for species richness of woody plants in the Chaco Dry Forest support the habitat amount hypothesis (HAH) (Fahrig, 2013), adding to the empirical research that supports the HAH (Watling et al., 2020). Our results also support the common finding that effects of habitat amount on species richness are stronger than effects of habitat fragmentation *per se* (Fahrig, 2003). In addition, the fragmentation effect, though weak, was positive, *i.e.* species richness increased very slightly with fragmentation *per se*, which is also consistent with most previous results across taxa (Fahrig, 2017).

Our study supports previous evidence of higher plant species richness in landscapes where there is more habitat (Cagnolo et al., 2006). This is consistent with the sample area effect as described in Fahrig (2013)A larger sample area (more habitat) contains more individuals and, for a given abundance distribution, this implies more species. Although our sample plots were all the same size, a larger amount of forest in the surrounding landscape “samples” more individuals and therefore a larger number of potential species from the ecoregion's species abundance distribution. This leads to a larger potential number of species immigrating into the sample plot, producing more species in sample plots in landscapes with more habitat than in those with less habitat. We are unaware of other studies testing the habitat amount hypothesis for woody species richness in subtropical dry forests but our results are consistent with studies of plant species diversity in other ecosystems (*e.g.*, Brazilian canga - Gastauer et al., 2021; Northern American savannas - Alofs et al., 2014).

We emphasize here that, although habitat fragmentation usually results from a process of habitat loss (Haila, 1999, 2002; Villard and Metzger, 2014), as is the case in Chaco forests (Carranza et al., 2015), the same degree of habitat loss can lead to very different degrees of habitat fragmentation (number of patches). Therefore, the independent effects of habitat amount and fragmentation can be evaluated by selecting sample landscapes such that the amount and fragmentation of habitat are uncorrelated. Thus, our sampling design does not confound the effects of habitat amount with the effects of fragmentation as many previous studies have done, and adds to the scarce literature that controls for both factors (Fahrig, 2003). However, due to the inherent costs of sampling multiple landscapes across a large area (Povak, 2012; Torrella et al., 2013), as usually occurs with landscape-scale studies, we had a relatively low sample size (24 landscapes, of which 8 were truly spatially independent landscapes), which precluded performing more complex statistical analyses. McGarigal and Cushman (2002) acknowledge this difficulty and recommend a general approach for handling this problem of low replication by using GIS queries and existing landscape analysis software. We used these techniques when selecting the landscapes studied and due to the high heterogeneity of biophysical variables in the Chaco region it was not possible to increase the number of landscapes at a meaningful spatial scale. Thus, the results obtained here are informative for the region studied but should not be directly extrapolated to other regions.

Our analyses of species richness also indicated a lagged relationship between habitat amount and species richness, as species richness in 2017 was more strongly related to habitat amount in 2009 than to habitat amount in 2017. This suggests a gradual loss of species in response to habitat loss, as has been shown for *Libidibia paraguariensis* and *Schinopsis lorentzii* (two highly valued species), which respond to forest amount with almost a decade-long lag (Appendix 7). Notably, there was no time-lag response to forest fragmentation *per se*, with standardized coefficients almost identical for the two time periods. Therefore, the lack of fragmentation effects on species richness in our results is not due to insufficient time since the patches were created through habitat loss. Note that the same result was found for a variety of taxa and systems in Fahrig (2020).

The best models of species richness explained approximately 22 % of the variance, pointing to additional (unmeasured) variables influencing biodiversity of woody vegetation in Chaco forests. In particular, variation in local site conditions such as land use history, soil type and conditions, and topography, affecting seed germination, plant growth, and pollination likely play a large role in explaining the variability among sites. In addition, variables influencing the persistence of the seed bank such as seed coat dormancy may be important (Khurana and Singh, 2001).

4.2. Species composition and trait density

Perhaps the most novel aspect of this study is our finding of much stronger evidence for effects of fragmentation *per se* on species composition than on species richness. Based on the correlations of species with landscape metrics (Appendix 7), some species such as *A. quebracho blanco, C. coccinea, L paraguariensis, M. salicifolia* and *S. lorentzii* are highly correlated with the amount of forest, while others such as *M. tweedianna, S. balansae, S bumelioides* and *S. praecox* are positively correlated with the number of patches. Interestingly, *J. rhombifolia* and *M. tweediana* are more likely to occur in forest plots in landscapes with scarce forest cover (Appendix 7). Hertzog et al. (2019) found effects on plant species composition of an index that combines habitat amount and fragmentation. However, ours is the first study to evaluate effects on plant species composition of fragmentation *per se*, *i.e.*, measuring fragmentation at a landscape scale and controlling for the effect of habitat amount (see Echeverría et al. (2007) for patch-scale studies). Some of our findings may be due to different species thriving in forest edges than those in forest interiors. Although all of our sample sites were in forest interiors, fragmented landscapes with many small patches have more forest edge, and so there may be more immigration of edge-related species into forest interior plots in landscapes with many small patches than in landscapes with a few large patches. This might explain our observed negative effect of fragmentation *per se* on leaf and seed size. Edge species typically have smaller seeds (Tabarelli et al., 2010), and a hotter environment at edges may favour species having small leaves and therefore less water loss (Zambrano et al., 2019).

Contrary to our prediction, we found a higher abundance of trees with high wood density in landscapes with more small patches. As our predictions were based on common attributes of forest edge species, it seems that the increase in wood density in response to fragmentation *per se* is related to some mechanism other than edge effects. A possible explanation for this finding is that small forest fragments usually remain within large properties where access for timber and charcoal extraction is restricted. Thus, after many years without logging, hardwood tree species can recover in small fragments within large agricultural properties. Torrella et al. (2013) also found taller species in more fragmented landscapes, which is consistent with this explanation. We also note that wood density is the only species composition or trait density response showing a time lag, in this case to habitat amount. The positive response of wood density to habitat amount was much stronger when habitat amount was measured in 2009 than when it was measured in 2017.We suggest that further work will be needed to shed light on these responses of wood density to habitat amount and fragmentation *per se*.

Overall our results suggest that while habitat fragmentation *per se* does not reduce species richness, it favours an assemblage of species that have different characteristics than those in landscapes with few large patches. This could then influence ecosystem function, as suggested by Hertzog et al. (2019), and thereby possibly alter ecosystem services (Conti et al., 2018). For example, shrub species with smaller leaves favoured by fragmentation *per se* might indicate lower primary productivity (Ordway and Asner, 2020). The increase in smaller-seeded species, typically wind-dispersed, might imply less food resources for animal species with increasing fragmentation *per se* (Wunderle, 1997). Finally, the higher wood density in landscapes with higher fragmentation *per se* suggests that such landscapes may provide higher carbon storage than landscapes with few large forest patches.

We found no evidence for lag effects of fragmentation *per se* on species composition or plant traits. We note that this was not due to a smaller change in habitat fragmentation *per se* than in habitat amount over time (Appendix 9). In fact, the median increase in fragmentation *per se* between 2009 and 2017 was 21 %, while the median decline in habitat amount was 8 %.

4.3. Conclusions and implications

Consistent with the habitat amount hypothesis, we found that forest amount increased plant species richness while forest fragmentation *per se* did not. In addition, species richness showed a delayed response to declining forest amount, suggesting an even greater effect of forest loss on plant species richness than would be inferred from comparing species richness to current forest levels. In contrast, fragmentation *per se* was a stronger determinant of species identity (composition) than forest amount, and we found no evidence for a time lag in this response.

Our results challenge the assumption that small forest patches in human-dominated landscapes have low conservation value. Various stakeholders (researchers, farmers, policy-makers) argue that such small patches have lost their conservation value and therefore should be “sacrificed” (*i.e.* cleared) to increase land-use intensity (*e.g.* Edwards et al. (2012)). In fact, a forest conservation law in Argentina has classified most forest patches in human-dominated landscapes as areas where deforestation is allowed (Aguiar et al., 2018; Camba Sans et al., 2018). Contrary to such policies, our results add to growing evidence for the conservation value of small forest fragments (Riva and Fahrig, 2022; Torrella et al., 2013; Wintle et al., 2019) and emphasize the need for conserving the most forest possible regardless of patch sizes.

Declaration of competing interest

This statement is to certify that:

The work is all original research carried out by the authors. All authors agree with the contents of the manuscript and its submission to the journal.

No part of the research has been published in any form elsewhere.

The research featured in the manuscript does not relate to any other manuscript of a similar nature that we have published, is in press, submitted or will soon be submitted to Biological Conservation or elsewhere.

The manuscript is not being considered for publication elsewhere while it is being considered for publication in this journal.

Any research in the paper not carried out by the authors is fully acknowledged in the manuscript.

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All appropriate ethics and other approvals were obtained for the research.

Data availability

Data will be made available on request.

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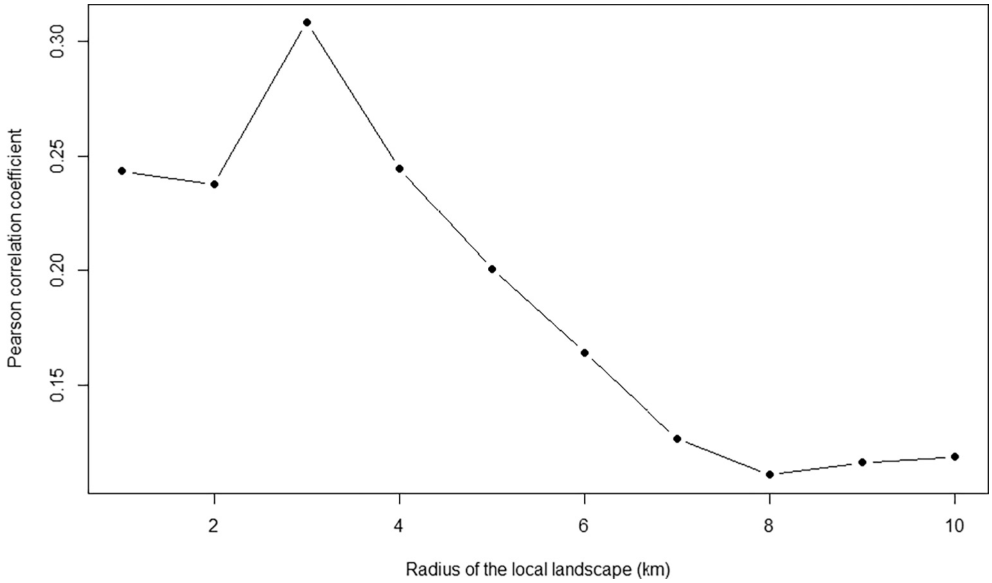
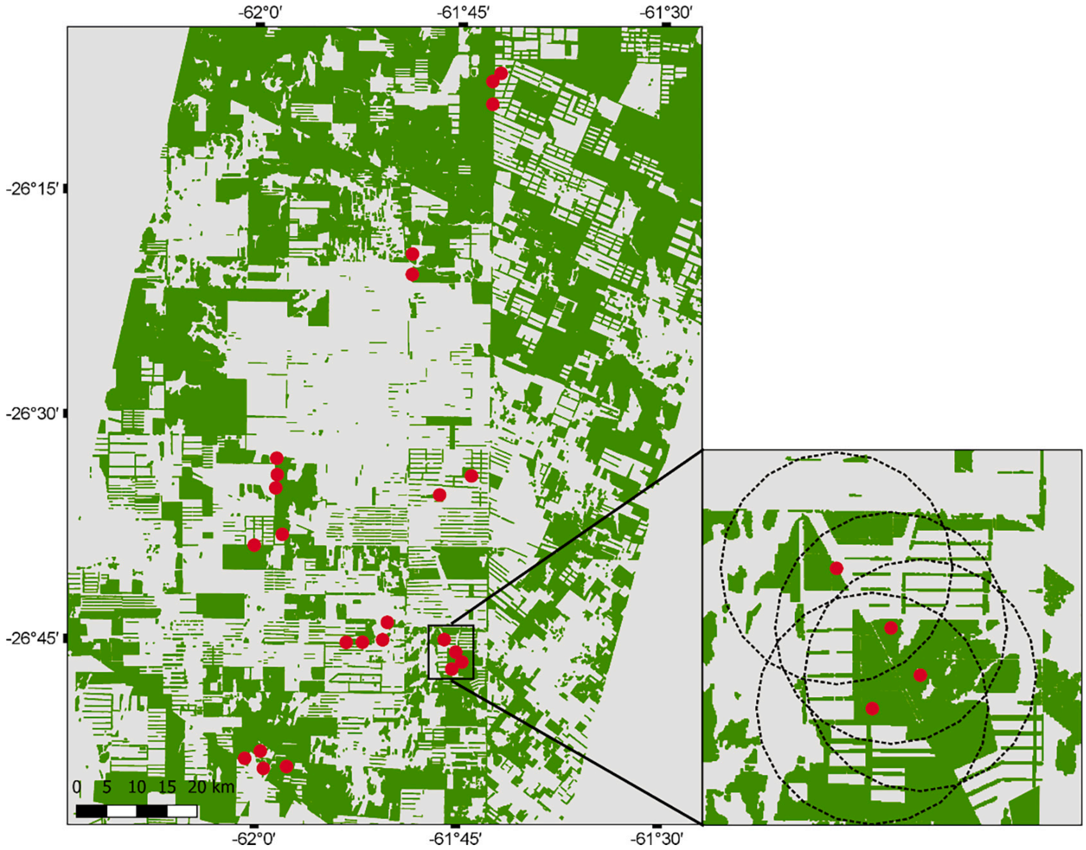
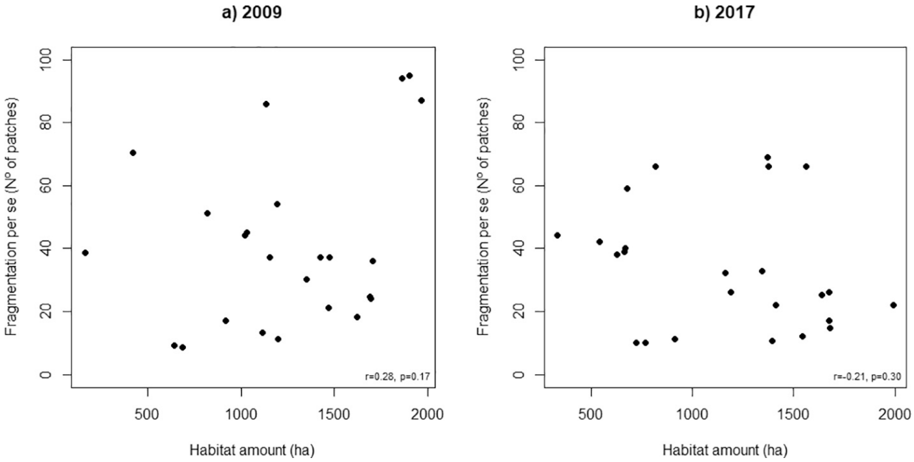
Appendix A



Appendix 1. Determination of the size of the local landscape for testing the habitat amount hypothesis in Chaco dry forests. The relationship between species richness of woody plants and habitat amount is strongest when habitat amount is measured within a radius of 3 km from the sample plots.



Appendix 2. Location of the 24 sample points. Dotted black circles represent local landscapes around each sample point.



Appendix 3. Relationship across the 24 sites between forest amount and fragmentation *per se* (number of patches) in 2009 and 2017. Correlation coefficient was 0.28 in 2009 and -0.21 in 2017.

Appendix 4

Trait values for leaf area, wood density, growth form and seed dry mass of 23 species sampled. Second line specifies trait ID in the TRY database.

Trait	Leaf area (mm^2)	Stem Specific Density (g/cm^3)	Growth form	Growth form consensus	Seed dry mass (g)
Trait ID (TRY database)	3113	4	42	6544	26
Aspidosperma quebracho blanco	127.99	0.73	Tree	0.97	2.00
Castela coccinea	675.00		Shrub	0.71	
Celtis pallida	675.00	0.60	Shrub		17.60
Jodina rhombifolia	116.54	0.61	Tree		
Libidibia paraguariensis	17.00	1.05	Tree		166.67
Maytenus spinosa	71.66	0.71	Shrub	0.70	
Mimosa detinens			Tree	1.71	
Morisonia atamisquea	5.23	0.80	Shrub	1.00	

(*continued on next page*)

Appendix 4 (*continued*)

Trait	Leaf area (mm^2)	Stem Specific Density (g/cm^3)	Growth form	Growth form consensus	Seed dry mass (g)
Morisonia retusa	675.00	0.61	Shrub		
Morisonia speciosa		0.66	Shrub	0.67	
Morisonia tweediana			Shrub	0.82	
Parkinsonia praecox	521.71	0.52	Tree		27.23
Prosopis kuntzei		1.09	Tree	1.00	
Prosopis nigra	18.32	0.76	Tree	0.93	1.00
Prosopis torquata	3.00	0.74	Shrub	1.00	
Sarcomphalus mistol	675.00	0.87	Tree	0.98	
Schinopsis balansae	675.00	1.03	Tree	1.00	
Schinopsis lorentzii	225.21	0.90	Tree	1.00	
Senegalia gilesii	576.85	0.81	Tree		
Senegalia praecox	11.32	0.76	Tree		
Solanum argentinum			Shrub	0.71	
Vachellia aroma	981.00	0.74	Tree		
Ximenia americana	1316.19	0.84	Tree	0.68	732.27

Appendix 5

Parameters of the models of the relationships between species richness, species composition, or density of traits and habitat amount (HAB) and fragmentation *per se* (FRAG) measured in 2009 and 2017.

Predictor variable	Response variable	Intercept	Estimate	Std Error	Confidence Interval (95 %)		R2	AIC	Std Error
Species richness		2.540						118.760	
	HAB 2009		0.094	0.059	−0.002	0.193	0.220	118.210	0.059
	FRAG 2009		0.021	0.057	−0.074	0.115	0.011	129.620	0.057
	HAB 2017		0.038	0.058	−0.057	0.134	0.036	120.330	0.058
	FRAG 2017		0.015	0.058	−0.081	0.110	0.006	120.69	0.058
Species composition (DCA1)		−0.029						51.016	
	HAB 2009		0.059	0.139	−0.171	0.288	0.008	52.822	0.139
	FRAG 2009		0.152	0.136	−0.072	0.376	0.053	51.700	0.136
	HAB 2017		0.057	0.139	−0.172	0.287	0.0075	52.834	0.139
	FRAG 2017		0.149	0.136	−0.075	0.374	0.051	51.750	0.136
Species composition (DCA2)		0.049						38.151	
	HAB 2009		0.078	0.106	−0.095	0.253	0.024	39.553	0.106
	FRAG 2009		0.267	0.090	0.118	0.417	0.282	32.178	0.090
	HAB 2017		−0.118	0.104	−0.290	0.053	0.055	38.784	0.104
	FRAG 2017		0.287	0.088	0.142	0.432	0.326	30.662	0.088
Wood density		1.972						−8.627	
	HAB 2009		0.069	0.037	0.008	0.131	0.135	−10.123	0.037
	FRAG 2009		0.048	0.039	−0.016	0.112	0.064	−8.227	0.039
	HAB 2017		0.001	0.040	−0.065	0.067	0.0001	−6.627	0.040
	FRAG 2017		0.056	0.038	−0.007	0.119	0.087	−8.828	0.038
Growth form		2.083						−17.079	
	HAB 2009		0.009	0.033	−0.045	0.065	0.0038	−15.172	0.033
	FRAG 2009		0.032	0.033	−0.021	0.087	0.042	−16.126	0.033
	HAB 2017		0.006	0.033	−0.049	0.062	0.167	−15.119	0.033
	FRAG 2017		0.021	0.033	−0.033	0.077	0.018	−15.528	0.033
Leaf area		4.732						−21.501	
	HAB 2009		0.045	0.029	−0.003	0.093	0.096	−21.931	0.029
	FRAG 2009		−0.045	0.029	−0.093	0.002	0.098	−21.987	0.029
	HAB 2017		0.042	0.029	−0.006	0.091	0.085	−21.650	0.029
	FRAG 2017		−0.054	0.028	−0.102	−0.007	0.142	−23.186	0.028
Seed dry mass		2.719						42.955	
	HAB 2009		−0.061	0.117	−0.255	0.132	0.012	44.657	0.117
	FRAG 2009		−0.166	0.113	−0.352	0.019	0.089	42.708	0.113
	HAB 2017		0.017	0.118	−0.177	0.212	0.001	44.932	0.118
	FRAG 2017		−0.168	0.113	−0.354	0.017	0.091	42.640	0.113

Appendix 6

Species scores of the first two axes of the Detrended Correspondence Analysis (DCA) calculated using the Bray-Curtis similarity index (Hill and Gauch, 1980) on the plots × species frequency matrix [24 × 25].

	Axis 1	Axis 2
A. quebracho blanco	0.244	−0.308
C. coccinea	−0.239	0.384
C. pallida	0.674	−0.086
J. rhombifolia	0.772	−1.588
L. paraguariensis	1.619	−2.447
M. atamisquea	−1.436	−1.537

(*continued on next page*)

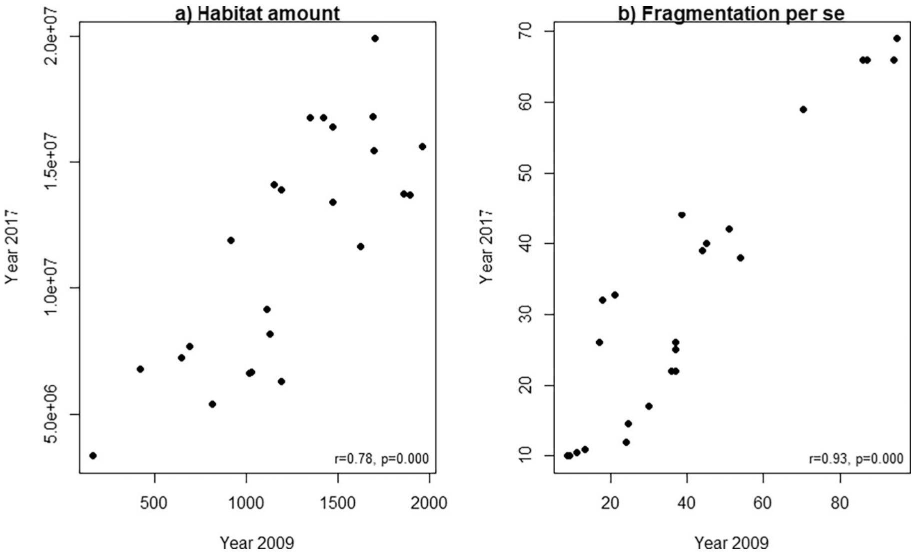
Appendix 6 (*continued*)

	Axis 1	Axis 2
M. detinens	1.279	−0.789
M. retusa	−0.947	0.638
M. salicifolia	1.771	1.495
M. speciosa	−1.406	0.930
M. spinosa	−1.044	−0.921
M. tweediana	−0.012	1.769
P. kuntzei	1.469	−0.162
P. nigra	1.431	1.247
P. praecox	2.626	0.858
P. torquata	−0.755	1.110
S. argentinum	1.080	−0.384
S. balansae	−1.077	2.825
S. bumelioides	0.898	−0.332
S. gilesii	−2.779	0.021
S. lorentzii	−1.129	−1.372
S. mistol	−1.479	−0.857
S. praecox	0.231	1.322
V. aroma	2.027	0.986
X. americana	0.745	−1.464

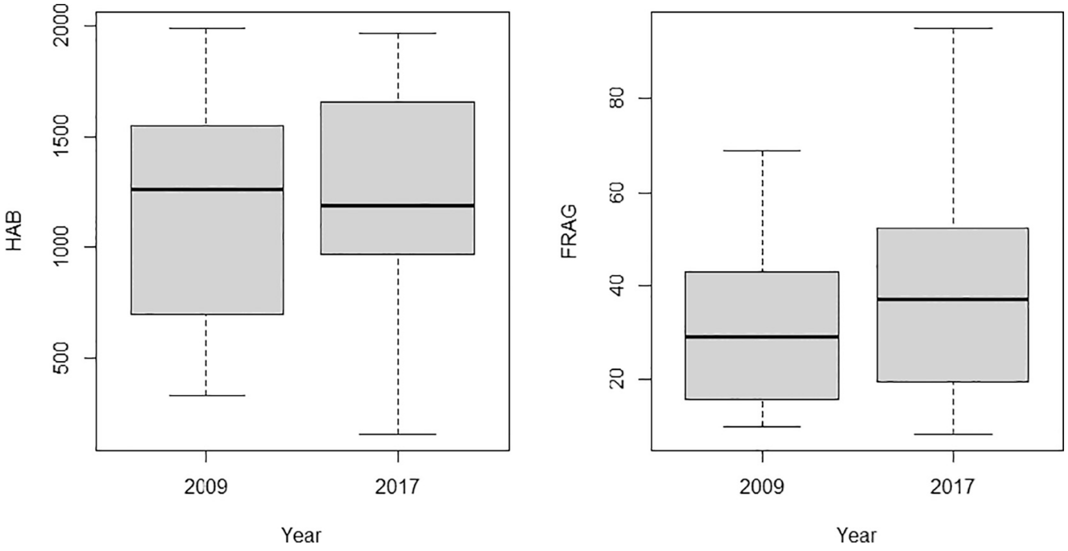
Appendix 7

Pearson correlation coefficients between the abundance of each species in 2017 and the landscape and patch metrics measured in 2009 and 2017: HAB, forest amount within 3 km of the plant sample plots; FRAG, number of forest patches within 3 km of the plant sample plots; AREA, area of the forest patch containing the sample plot; DIST, distance of the patch containing the sample plot to the nearest other forest patch.

	a) 2009				b) 2017			
	HAB	FRAG	AREA	DIST	HAB	FRAG	AREA	DIST
A. quebracho blanco	0.16	−0.27	0.30	0.15	0.20	−0.25	0.02	−0.20
C. coccinea	0.33	−0.19	0.32	−0.07	0.40	−0.28	0.40	0.00
C. pallida	0.10	−0.08	0.16	0.11	0.14	−0.09	−0.16	−0.18
J. rhombifolia	−0.38	0.06	−0.14	0.28	−0.30	0.13	−0.19	0.11
L. paraguariensis	0.31	−0.04	−0.07	−0.21	0.49	−0.12	−0.06	−0.21
M. atamisquea	0.14	−0.19	0.05	−0.30	0.18	−0.23	0.20	−0.09
M. detinens	0.20	−0.21	0.22	−0.06	0.32	−0.20	0.10	−0.12
M. retusa	0.05	−0.14	0.16	0.01	−0.15	−0.12	0.27	0.05
M. salicifolia	0.28	0.08	0.23	−0.06	0.02	0.22	0.04	−0.09
M. speciosa	0.11	−0.06	−0.18	−0.17	0.13	−0.12	−0.13	−0.11
M. spinosa	0.25	−0.17	0.05	−0.08	0.41	−0.33	0.21	−0.05
M. tweediana	−0.02	0.33	−0.22	0.20	−0.26	0.29	−0.32	−0.13
P. kuntzei	0.16	−0.01	0.01	0.04	0.26	−0.07	−0.06	−0.02
P. nigra	0.03	−0.11	0.04	0.16	−0.02	−0.02	0.24	0.54
P. praecox	0.08	−0.09	−0.15	−0.11	0.11	−0.06	0.02	0.22
P. torquata	0.05	−0.21	0.40	0.07	−0.02	−0.12	0.41	0.17
S. argentinum	−0.12	0.04	0.09	0.27	−0.08	0.10	−0.16	−0.11
S. balansae	0.25	0.62	−0.29	−0.11	−0.01	0.57	−0.28	−0.15
S. bumelioides	0.26	0.35	−0.18	−0.13	0.36	0.29	−0.17	−0.23
S. gilesii	0.07	−0.30	0.37	−0.11	0.12	−0.35	0.53	−0.01
S. lorentzii	0.32	−0.24	0.05	−0.18	0.41	−0.36	0.14	−0.02
S. mistol	0.03	−0.09	−0.02	−0.08	0.10	−0.15	0.15	0.05
S. praecox	0.13	0.33	−0.15	−0.05	−0.13	0.34	−0.42	−0.31
V. aroma	0.19	−0.01	0.03	−0.21	0.23	0.01	0.00	−0.13
X. americana	−0.08	−0.06	−0.07	0.13	−0.10	−0.08	−0.14	−0.15



Appendix 8. Relationship between forest amount in 2009 and 2017 and between forest fragmentation *per se* (number of forest patches) in 2009 and 2017. Both forest amount and fragmentation *per se* were measured in circular landscapes of radius 3 km surrounding 24 plant sample plots.



Appendix 9. Change in forest amount (HAB: ha) and fragmentation *per se* (FRAG: number of patches) from 2009 to 2017.

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