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Research Paper

Measuring forest fragmentation using multitemporal forest cover maps: Forest loss and spatial pattern analysis in the Gran Chaco, central Argentina

Maria Laura Carranza[a], Laura Hoyos[c], Ludovico Frate[a,b,*], Alicia T.R. Acosta[d], Marcelo Cabido[c]

[a] EnviX-Lab, Dipartimento di Bioscienze e Territorio, Università degli Studi del Molise C.da Fonte Lappone, 86090 Pesche, IS, Italy
[b] Istituto di Biologia Agro-Ambientale e Forestale, CNR/IBAF, Monterotondo, Roma, Italy
[c] Instituto Multidisciplinario de Biologıa Vegetal (UNC-CONICET) and Facultad de Ciencias Exactas, Fisicas y Naturales (Universidad Nacional de Cordoba), Av. Velez Sarsfield 299, C.C. 495, 5000 Cordoba, Argentina
[d] Dipartimento di Scienze, Università degli Studi di Roma Tre, V.le Marconi 446, 00146 Roma, Italy

HIGHLIGHTS

- Forest loss and spatial pattern changes by sampling multi-temporal land cover maps.
- Pattern metrics show index-specific relationships with forest cover.
- Significant forest loss occurs along with significant changes in pattern metrics.
- Useful information for land management and fragmentation-prevention issues.

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ABSTRACT

Forest fragmentation is a landscape-level process that consists of two interdependent components: forest loss and spatial pattern changes to which species respond differently. Efficient programs to conserve native biodiversity require a sound understanding of the relation between forest cover and the spatial pattern of forest fragments, but these issues remain almost unknown for subtropical ecosystems. We examine the forest fragmentation of the Gran Chaco in central Argentina over the last 30 years. In particular, we quantify forest loss and spatial pattern changes using random sampling techniques on multi-temporal forest cover maps (1979, 1999 and 2010). We analyzed forest fragmentation according to the following steps: (i) selection of fragmentation pattern indices (PIs), (ii) sampling on forest cover maps and PIs calculation, (iii) statistical comparison by bootstrapping, and (iv) trajectory analysis. During the last three decades, forest cover declined dramatically (∼90%) and the selected pattern metrics (MPS, PD, ED) varied significantly ($p < 0.05$). The results depict a devastating situation of Gran Chaco forests with a progressive reduction to few small fragments during the last decades. Furthermore when forest loss exceeded the ∼50% of the total land area, the temporal trajectories of the selected PIs underwent an abrupt change. Distinguishing habitat spatial pattern changes from forest loss over time supports the identification of specific conservation actions and provide the basis to establish the lower threshold of forest cover and the more effective arrangement of fragments necessary to mitigate the fragmentation effects.

1. Introduction

Forest ecosystems have played a major role in human history, and forest fragmentation has accompanied population growth and development throughout the world for thousands of years (Food and Agricultural Organization of the United Nations, 2012). The extent of fragmentation, which has affected many natural forests

* Corresponding author at: EnviX-Lab, Dipartimento di Bioscienze e Territorio, Università degli Studi del Molise, C.da Fonte Lappone, 86090 Pesche, IS, Italy.
E-mail addresses: carranza@unimol.it (M.L. Carranza), laurahoyos@gmail.com (L. Hoyos), ludovico.frate@unimol.it (L. Frate), acosta@uniroma3.it (A.T.R. Acosta), mcabido@imbiv.unc.edu.ar (M. Cabido).

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worldwide, constitutes one of the most serious causes of biodiversity loss, which in turn greatly influences ecosystem structure and function. Recent studies have indicated that fragmentation has several negative (Trombulak et al., 2004) and long-lasting (Flaspohler et al., 2010; Turner, 1996) environmental and ecological consequences: it affects ecosystem functions, such as hydrological cycles and soil dynamics (Rudel et al., 2005), climate regulation (Houghton et al., 2000; Nabuurs, Schelhaas, Mohren, & Field, 2003) and biodiversity (see Fahrig, 2003 for a review).

According to the patch-corridor-matrix model (Forman, 1995), forest fragmentation can be seen as a landscape-level process in which a large, intact area of a single forest type is progressively subdivided into smaller, geometrically altered and isolated patches (Fahrig, 2003; Forman & Godron, 1986; McGarigal, Cushman, & Regan, 2005). Forest fragmentation consists of two components: forest loss and changes in the spatial pattern (i.e. pattern metrics) (Fahrig, 2003; Long, Nelson, & Wulder, 2010; Neel, McGarigal, & Cushman, 2004). Forest loss and spatial pattern changes are the two most important factors in the current species extinction event at global scale (Fahrig, 1997; McGarigal et al., 2005). In response, there is a growing mandate among natural resource managers to evaluate the impacts of proposed management actions on habitat fragmentation (Long et al., 2010; Wang, Blanchet, & Koper, 2014). Thus, new guidelines to help managers to understand the many complex issues involved in the assessment of habitat fragmentation are urgently needed. For instance, if in a given landscape forest loss results in a constant number of smaller patches, then fragmentation effects on biodiversity are due to forest loss alone. Only when the number of patches increases by the breaking apart of forests do we find that both forest loss and spatial pattern (decreasing size and increasing isolation of forest patches) are involved. On the other hand, when forest amount is constant over time, changes in spatial pattern generally has either no effect or a negative effect on forest species survival (Fahrig, 1997; Gavish, Ziv, & Rosenzweig, 2012).

The Gran Chaco, which is among the largest seasonally dry subtropical forests in the world, (ca. 1,200,000 km^2), occurs in Argentina, Paraguay and Bolivia (Bucher, 1982; Zak, Cabido, Cáceres, & Diaz, 2008). It comprises one of the few areas worldwide where the transition between the tropics and the temperate belt does not occur in the form of a desert but as semi-arid forests and woodlands (Morello & Adamoli, 1974; Prado, 1993). These subtropical seasonally dry forests are characterized by a specific vegetation and fauna that determines consistent biodiversity values (Cagnolo, Cabido, & Valladares, 2006; Molina, Valladares, Gardner, & Cabido, 1999; Torrella, Ginzburg, Adámoli, & Galetto, 2013). Moreover, these forests provide numerous ecosystem services (Conti & Díaz, 2013) that are necessary for the subsistence of local communities and the regional economy (Cáceres, 2014; Zak et al., 2008). Despite many outstanding features that make these complex ecosystems worthy of protection, the Chaco forest is a poorly represented ecoregion in the Argentinean and South American protected area systems (Izquierdo & Grau, 2008; Matteucci & Camino, 2012). Furthermore, the current legal regulation for the region, which is crucial for generating practices to mitigate the impacts of forest fragmentation, is liberal and permissive, thereby promoting deforestation (Mastrangelo & Gavin, 2012; Torrella et al., 2013). The generalized expansion of agriculture, driven by global trends in technology and soybean markets (Grau, Gasparri, & Aide, 2005) and by global changes in precipitation regimes (Hoyos et al., 2013; Zak et al., 2008), has promoted the clearing of approximately 6 million ha of native forest over the last three decades (Grau & Aide, 2008; Torrella et al., 2013). In particular, the generalized expansion of anthropic land uses are related to the sharp drop of the Gran Chaco natural ecosystems which lead the exiting protected areas to a worrying ecological isolation (Matteucci & Camino, 2012). Although efficient programs to conserve forest biodiversity in fragmented landscapes require a sound understanding of the evolution and spatial distribution of the size of forest fragments over time (Zuidema, Sayer, & Dijkman, 1996), these issues remain almost unknown for the Gran Chaco forests. Regional patterns of forest fragmentation have been recently described in different sectors of the Gran Chaco (e.g., Grau et al., 2005; Hoyos et al., 2013; Zak et al., 2008) but fragmentation studies accounting of the relation of forest loss and spatial pattern changes over time are still necessary.

Thus, the purpose of this paper is to examine the forest fragmentation of the Gran Chaco over the last 30 years accounting for the interdependencies between forest loss and spatial pattern changes. The research, based on multi-temporal land cover maps (1979, 1999 and 2010) of central Argentina addressed the following questions: (i) How did forest cover change? (ii) How did forest spatial pattern vary? (iii) Which is the relative importance of forest loss and spatial pattern on the fragmentation process?

In particular, we quantify forest loss and spatial pattern changes using random sampling techniques on multi-temporal maps followed by a bootstrapping significance test (Fortin, Jacquez, & Shipley, 2012; Manly, 2006). In order to investigate the relationship between forest loss and spatial pattern changes over time we built specific bidimensional 'relationship spaces' (*sensu* Long et al., 2010) in which the variation of spatial pattern metrics (e.g. mean patch size, patch density, edge density) were plotted against different levels of forest cover. We assumed that the relative importance of forest loss and spatial pattern varies through space and time. By identifying the role of forest cover and configuration changes, we contribute to the in-depth description of the process of fragmentation of the Gran Chaco over the last 30 years and we provide the basis for the formulation of a scientifically sound hypothesis about their effects on biodiversity. For instance, specific thresholds of forest cover could be crucial in determining temporal changes on pattern metrics, which might promote irretrievable losses on forest biodiversity and functionality. By interpreting the observed forest cover and spatial pattern changes, and their non linear relationships we contribute to stress the ecological value of the remaining forest patches in order to prioritize conservation efforts in this fragile and highly vulnerable ecosystem.

2. Material and methods

2.1. Study area

The study area is located at the southern extreme of the dry Chaco, to the northeast and northwest of Cordoba Province, in central Argentina (Fig. 1), and it belongs to the Chaco Phytogeographical Province (Cabrera, 1976). Its lowlands were formerly dominated by *Aspidosperma quebracho-blanco* Schlecht and *Schinopsis lorentzii* (Cris.) Engl. subtropical seasonally dry forests (Bonino & Araujo, 2005; Zak & Cabido, 2002). At present, the non-cultivated area is covered mostly with secondary semi-deciduous forests and shrub lands, alternating with patches of old-growth forests and open shrub lands. The plant communities in the arid and semi-arid Chaco of Cordoba are known in detail from the works of Cabido, Acosta, Carranza, and Diaz (1992), Cabido, González Albarracín, Acosta, and Díaz (1993), Cabido, Manzur, Carranza, and González Albarracín (1994), Carranza, Cabido, Acosta, and Páez (1992) and Zak and Cabido (2002). While forest loss and conversion have affected the species richness of both plants and animals (Cabido et al., 1994; Gardner, Cabido, Valladares, & Diaz, 1995), well-conserved forest patches have been reported to comprise the highest alpha diversity in the area (Cagnolo, Valladares, Salvo,

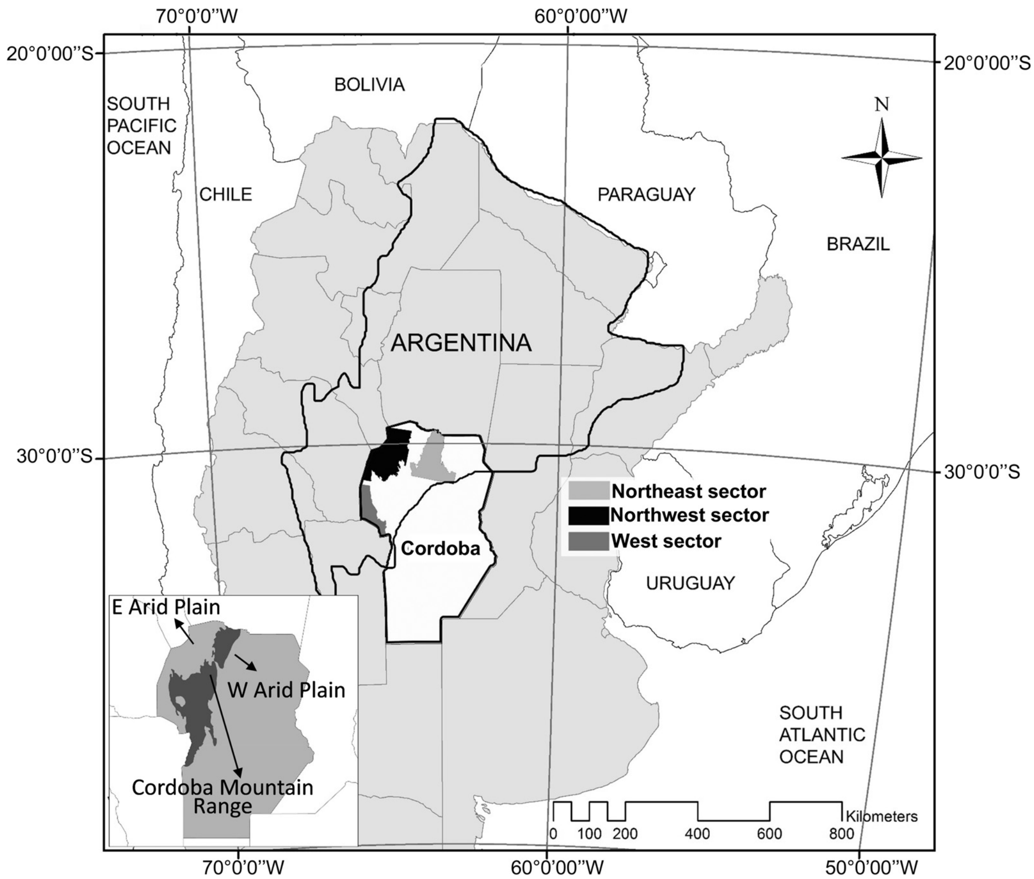

Fig. 1. Location of the Great Chaco (black line), Cordoba Province (white), and the three study sectors (gray shades) in Argentina.

Cabido, & Zak, 2008) and to provide more efficient ecosystem services, such as carbon storage (Conti & Díaz, 2013). We sampled a wide area of almost three million hectares in central Argentina that are representative of the Gran Chaco landscape and the main processes that have shaped it over the last decades (Hoyos et al., 2013). The area is organized into three sectors, which are designated as 'West' (W), 'Northwest' (NW) and 'Northeast' (NE) (Fig. 1). The first two sectors are arid plains located on the west of Cordoba mountain range, and the last one occupies the east of the same range (eastern semi-arid plain).

The climate is warm temperate to subtropical, with a mean annual temperature ranging from 16 °C in the northeast to 19 °C in the northwest and west; the mean annual rainfall decreases in the same direction from more than 800–500 mm (Zak et al., 2008). A pronounced water deficit exists in the west of the area (Hoyos et al., 2013; Zak et al., 2008). In the case of the northeast sector, the recent increase in annual precipitation, specifically during the growth period, has made crop production possible and profitable; this was not the case in the west sector, where crop production is not possible without irrigation (Hoyos et al., 2013). Indeed, Zak et al. (2008) and Hoyos et al. (2013) reported lower deforestation in the NW and W sectors, primarily related to logging for nonagricultural purposes, such as the extraction of firewood and timber and clearing for natural pastures (Carranza et al., 1992).

2.2. Forest cover maps

Forest cover maps were derived from existing large-scale land cover maps of the area relative to the years 1979, 1999 and 2010 (Hoyos et al., 2013). Zak and Cabido (2002), comparing remote sensed images and phytosociological field data, found a good correspondence between Landsat TM classification and vegetation types on the Gran Chaco. Thus, in this study the analysis of forest loss and configuration changes was based on land cover maps derived from previous studies (Hoyos et al., 2013). These maps were produced based on Landsat satellite images for the years 1979, 1999 and 2010 and extensive fieldwork for accuracy assessment (Congalton & Green, 1999). To identify the land-cover units, three Landsat MSS scenes from February 1979, three Landsat TM scenes from November 1999, and three Landsat TM scenes from March 2010 were used. All Landsat images were acquired during the vegetation growing season of the southern hemisphere. The spatial resolution of the maps was harmonized to the coarser map (1979), which had a pixel dimension of 79 m × 79 m. The classification of Landsat MSS and TM images resulted in reliable land-cover maps (overall accuracy 80%) composed of five vegetation classes: closed forest, open forest, shrublands, halophytic vegetation and cultural vegetation (croplands and urban areas). Further details on the construction of the digital maps, confusion matrices and their accuracy assessment can be found in Hoyos et al. (2013). For our analysis, we selected only closed forests from the other land-cover types. These forests correspond to lowland seasonally dry forests, with *Aspidosperma quebracho-blanco* Schlecht. (white quebracho; Apocinaceae) and *Schinopsis lorentzii* (Cris.) Engl. (red quebracho; Anacardiaceae) as dominant trees and a tree canopy of at least 50% cover (Hoyos et al., 2013) that according with Sayago (1969) comprise the potential vegetation of the area. The distribution of closed forests over time is reported in Fig. 2. A detailed description of seminatural cover types is beyond the scope of this paper but we

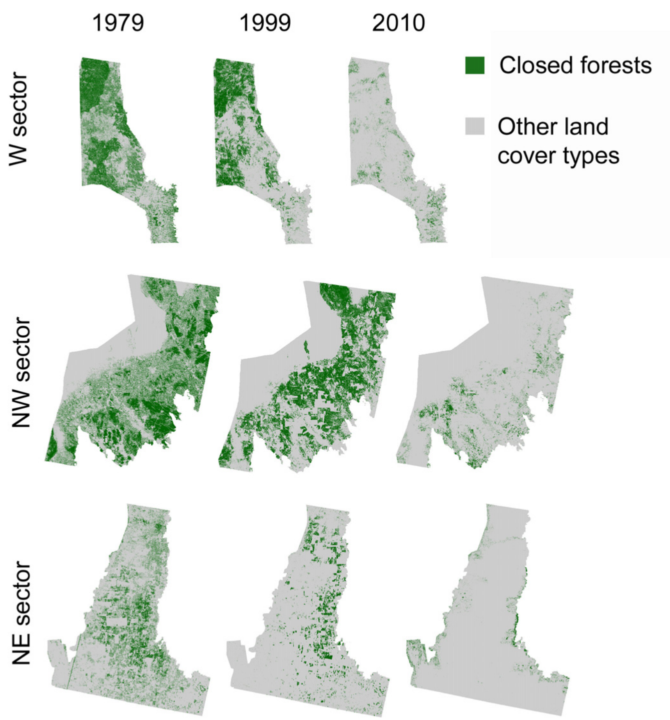

Fig. 2. Distribution of closed forests in the different sectors for the years 1979, 1999 and 2010.

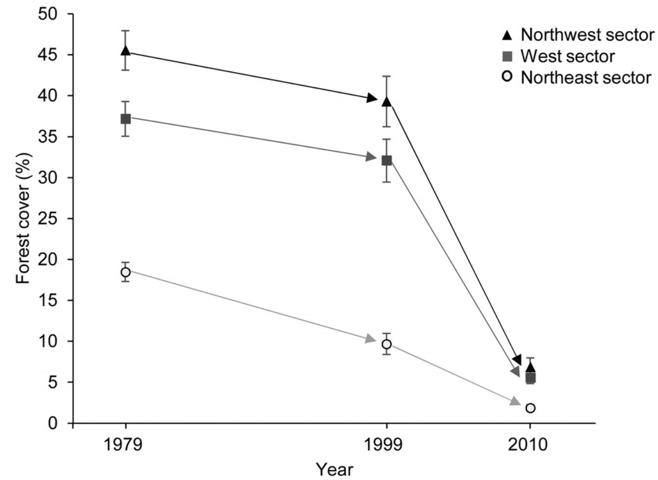

Fig. 3. Closed forest loss over time in the analyzed sectors. Percent of forest cover mean values estimated from randomly sampled (1 km × 1 km) units (symbol) and the 95% confidence intervals obtained using a bootstrap procedure (BCa) (error bars) are represented.

can briefly describe them as follows. Open forests (*Prosopis flexuosa* D.C. and *Mimozyganthus carinatus* (Griseb.) Burkart) are the product of both selective logging of closed forests and the re-growth of impoverished forests after disturbance, with less than 10% tree cover. Shrublands (*Larrea divaricata* Cav.) occur on disturbed sites, after pasture or agricultural abandonment and intense fire events, with high bare soil percentages. Halophytic vegetation is a complex mosaic dominated by succulent shrubs (mainly Chenopods) occurring in saline depressions.

2.3. Data analysis

We analyzed forest change over time (years 1979, 1999, 2010) in the southern extreme of the Gran Chaco, using a sample-based approach, which specifically accounts for the interdependencies between landscape composition and configuration changes. The chosen approach offers a sound frame to describe the relation between forest loss and spatial pattern changes (Carranza et al., 2014; Neel et al., 2004; Wang et al., 2014) that is crucial for a correct interpretation of the ongoing landscape processes (Frate et al., 2014; Hargis, Bisonette, & David, 1998). Moreover, the sample-based approach allows producing statistically valid estimates of forest cover and spatial pattern at regional and continental scales (Hassett, Stehman, & Wickham, 2012). The procedure consists of four sequential steps:

1. Selection of the fragmentation pattern indices (PIs): we selected a set of four non-redundant PIs that have been widely suggested in the literature for fragmentation analysis (Frate & Carranza, 2013; Haines-Young & Chopping, 1996; Uuemaa, Antrop, Roosaare, Marja, & Mander, 2009) and that have been previously reported to be adequate for sample-based estimations of landscape pattern (Hassett et al., 2012). In particular, after measuring the percent of the landscape covered by forests (%Forest), we calculated the following spatial pattern metrics: mean patch size (MPS), patch density (PD) and edge density (ED). McGarigal and Marks (1995) provided the formula for each of the selected PIs.
2. Landscape sampling and PI calculation: a set of non-overlapping square grid units was randomly sampled (totaling 10% of the total extent of each sector), and for each sampling unit, the selected fragmentation PIs were computed using FRAGSTATS (McGarigal & Marks, 1995). To avoid the border effect, only grid cells that were entirely included in the analyzed areas were considered. The analysis was performed at two plot dimensions: 1 and 10 km^2. The chosen dimensions were at least two times larger than the landscape grain (O'Neill et al., 1996).
3. Statistical comparison: the PI estimators (in our case, the arithmetic mean; see Hassett et al., 2012 for details) were calculated, and a bootstrap procedure (bias-corrected and accelerated bootstrap) was applied to obtain 95% confidence intervals (Fortin et al., 2012).
4. Trajectory analysis: the temporal trajectory of each sector was identified as follows. For all of the chosen fragmentation PIs, a specific relationship space (*sensu* Long et al., 2010) was produced by projecting all of the computed spatial pattern metric values (ED, PD and MP) per sampling plot against the percent of forest cover (%Forest). The construction of a multi-temporal relationship space derived from sampled landscapes offered sound insight for spatial configuration metrics (Long et al., 2010) and was used here in the forest fragmentation analysis. Then, the arithmetic mean of each of the selected PIs was plotted in the relationship space, and the temporal trajectories for each sector (W, NW, NE) were drawn by connecting PIs means chronologically with arrows.

3. Results

The proportion of forest cover in the Gran Chaco declined greatly over time (Fig. 3 and Table 1), and forest loss became particularly striking during the last decade (1999–2010). Thirty years ago, the percent cover of white and red quebracho forests was clearly higher in the analyzed sectors. In fact, in 1979, forest cover ranged from 45% of the area in the NW sector, to 37% in the W, to only 19% in the NE. Moreover, while in the first time period (1979–1999), the rate of change in forest cover looked very similar in all sectors (the trajectories in Fig. 3 are almost parallel), in the last time period

Table 1
Forest Pattern Indices (PIs) values in the West (W), Northwest (NW) and Northeast (NE) sectors for the years 1979, 1999 and 2010. PIs' arithmetic means, estimated from randomly sampled (1 km × 1 km) tiles, along with 95% confidence intervals obtained by a bootstrap procedure (BCa), are reported.

PIs	Sector	1979			1999			2010		
		Mean	Upper CI	Lower CI	Mean	Upper CI	Lower CI	Mean	Upper CI	Lower CI
% of forest	NE	18.46[a]	19.64	17.31	9.67[b]	10.97	8.40	1.85[c]	2.26	1.47
	NW	45.57[a]	47.93	43.11	39.31[b]	42.39	36.20	6.85[c]	7.97	5.68
	W	37.18[a]	39.29	35.06	32.09[b]	34.69	29.44	5.57[c]	6.33	4.84
Mean patch size	NE	5.01[a]	5.78	4.28	4.37[a]	5.30	3.47	0.30[b]	0.38	0.22
	NW	21.79[a]	24.91	18.81	23.90[a]	27.22	20.75	1.66[b]	2.41	1.01
	W	17.59[a]	19.95	15.26	15.66[a]	18.19	13.20	0.71[b]	0.81	0.61
Edge density	NE	47.50[a]	49.62	45.37	18.70[b]	20.62	16.78	7.10[c]	8.37	5.81
	NW	73.64[a]	76.58	70.59	56.10[b]	59.51	52.58	22.87[c]	25.77	20.08
	W	70.70[a]	73.02	68.34	61.19[b]	64.40	57.90	23.51[c]	26.14	20.97
Patch density	NE	6.43[a]	6.70	6.17	2.36[b]	2.57	2.14	1.55[c]	1.81	1.29
	NW	5.86[a]	6.22	5.50	4.30[b]	4.66	3.92	4.34[b]	4.81	3.88
	W	6.28[a]	6.64	5.92	6.94[a]	7.36	6.51	5.28[b]	5.76	4.79

a, b, c, indicate significant differences in the PIs' arithmetic means between the compared dates.

(1999–2010), it was accelerated for the western sectors (NW and W). In the most recent data, the percent of forest throughout the region was very low, with values of 1.9% for the NE, 6.9% for the NW and 5.6% for the W sector.

Spatial pattern metrics are characterized by index-specific behaviors in relation to white and red quebracho forest cover (Fig. 4a–c). For instance, as shown by the sample-based relationship space of MPS vs. % Forest (Fig. 4a), mean patch size tends to be very low for forest cover values below 50%; MPS values exponentially increase when the forest cover exceeds the 50%. Edge density is characterized by a symmetric parabolic relationship with forest cover (Fig. 4b). ED is low at high and at low forest cover values and presents a positive high peak at intermediate values of forests cover (~50%). Patch density has an asymmetric parabolic shape along the forest cover gradient (Fig. 4c). PD is very low for landscapes dominated by forests, tends to increase as the percent of forest cover declines, peaks when forest reaches almost 20% of the landscape area and declines as the forest cover becomes close to 0.

The temporal trajectories of each sector (W, NW, NE) into the specific relationship spaces, per 1 km sampling plot, are reported in Fig. 4. The general trends of PIs for the 10 km plots are similar to those for the 1 km case and are reported in Appendices 1 and 2. In correspondence with the evident decrease in forest cover that occurred in all three sectors, the spatial pattern metrics tended to vary significantly (Table 1). As observed for the forest cover, changes in the spatial pattern parameters occurred at lower rates in the first time period (1979–1999) and accelerated in the second one (1999–2010).

The temporal trajectories of MPS for the three sectors (NW, W and NE) were included in the decreasing tile of the relationship curve (forest cover below the 50%). The mean dimension of the white and red quebracho forest patches (MPS) in 1979 were largely different in the analyzed sectors and had high values in the NW (45.57), intermediate values in the W (37.18) and small values in the NE (18.46) (Table 1; Fig. 4a). While modest variations in the MPS values were evident in the first time period (1979–1999), the MPS values significantly decreased in the three sectors over the last time period (1999–2010), dropping to 1.66 ha in the NW, 0.71 ha in the W and 0.30 in the NE.

The edge density of the forests in the study area significantly decreased over time (Table 1; Fig. 4b). The projection of multitemporal ED estimators in the specific relationship space portrayed three temporal trajectories which are included in the decreasing left side of the parabolic relation curve. In the Northeast sector, the prior ED value collapsed from 47.50 to 7.10. In the other two sectors, although a significant reduction of ED also occurred, the magnitude of the change was less extensive. ED in the NW sector decreased from 73.63 to 22.87, and in the W sector, it decreased from 70.70 to 23.51. The variation in forest patch density (PD) over the last 30 years was less evident (Table 1; Fig. 4c). The projection of PD estimators in the specific relationship space portrayed temporal trajectories that move from the right to the left tile of the curve. During the first time period (1979–1999), significant reduction in the density of forest patches occurred on the NW (from 5.86 to 4.66) and NE (from 6.43 to 2.36) sectors, while in the W sector, the PD values remained almost constant (from 6.28 to 6.64). In the second time period, a weak but significant reduction of PD occurred in the NE (from 2.36 to 1.55) and W (from 6.94 to 5.28) sectors, which was less evident and not significant in the NW sector (from 4.30 to 4.34).

4. Discussion

Our results show that the drastic transformation of the Gran Chaco landscape that has occurred over the past decades (Hoyos et al., 2013; Zak et al., 2008) also gave rise to a conspicuous process of forest fragmentation. The statistical comparison of PIs over time not only confirmed the consistent process of forest loss, which was particularly striking in the last decade, but also pinpointed significant changes in the spatial pattern of the remaining forest patches. Focusing on only closed forest patches embedded in an ecologically neutral matrix might seem simplistic. However, the adopted perspective provides effective tools to quantify closed forest fragmentation and to describe their possible effects on forest specialist species (or "true forest species" *sensu* Hermy, Honnay, Firbank, Grashof-Bokdam, & Lawesson, 1999), namely, species which perceive closed forest remnants as suitable habitats and that are unable to survive in the surrounding matrix (Lövei, Magura, Tóthmérész, & Ködöböcz, 2006).

Trajectory analysis underlined differences on the relative importance of forest loss and spatial pattern changes through the analyzed sectors and time steps. Furthermore, when forest loss exceeded the ~50% of the total land area, the temporal trajectories of MPS and ED underwent an abrupt change. These transitions may seriously affect forest species abundance and richness. Recent evidences highlighted that, at intermediate levels of habitat amount, the spatial configuration of the remaining habitats plays a crucial role in species movement and persistence (e.g., Cushman, Shirk, & Landguth, 2012; Villard & Metzger, 2014). However, in the last time span (1999–2010), the amount of closed forest for the NE

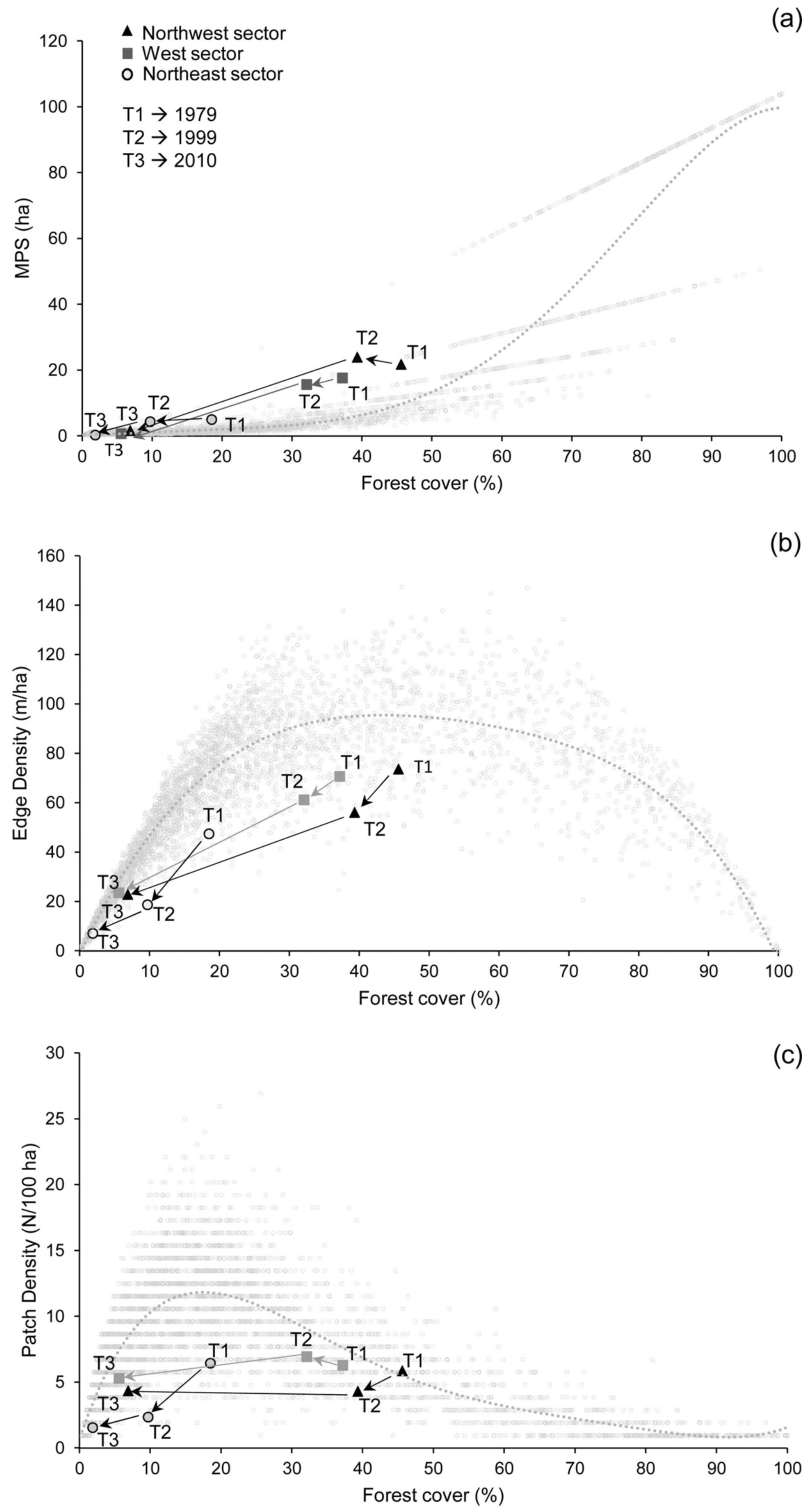

Fig. 4. Trajectories of closed forests in the relationship space given by the % forest cover and the other fragmentation PIs (MPS: mean patch size (a), ED: edge density (b) and PD: patch density(c)). Light gray dots represent the observed values of pattern metrics in the entire set of sampled (1 km × 1 km) grid units and symbols (squares, circles and triangles) indicate the arithmetic mean for each sector and date.

sector reached very low cover values, making the effect of spatial configuration negligible (Cushman et al., 2012).

The analysis of the forest mean patch size showed similar temporal changes in all of the analyzed sectors and depicted modest variations in the first time step followed by a remarkable process of forest fragmentation in the last decade. The constant value of MPS during the first time step despite the significant loss of forest cover, is most likely related to the removal of patches belonging to different class size categories (from small to very large). Note that forest patches scattered throughout the landscape, may serve as stepping stones, which are crucial for species dispersal enhancing the overall connectivity across the landscape (Saura, Bodin, & Fortin, 2014). Thus, the removal of entire patches, as in this case, probably reduces the chance for organisms to move from a patch of forest to another (Schumaker, 1996), promoting isolation effects and biodiversity loss across the entire landscape (Fahrig, 1997; McGarigal et al., 2005). The decrease in patch size which took place during the last decade highlighted a worrying forest fragmentation occurring across the entire landscape. The sharp drop in patch size depicts a landscape with small forest patches, the remnant nuclei of closed forests. Such changes could drastically affect the population dynamics of "true forest species" by altering the opportunity that organisms will gain access to habitat patches or by increasing extinction risks due to demographic, stochastic and genetic events (Bennett & Mulongoy, 2006; Cushman et al., 2012; Fahrig, 1997). The implications of this accelerated loss of large patches may have serious consequences for the biodiversity of Chaco forest where small fragments generally host few number of rare and specialist species (Cagnolo et al., 2008).

The sustained decline of ED values over time indicates the existence of shorter forest edges, which is clearly related to the reduction of closed forest cover on recent landscapes relative to past ones. When, as in our study, the percent of cover of forests in the prior situation is under 50% and continues to diminish over time, the forest edges also decrease. Many authors agree that small forest patches (<10 ha) are entirely influenced by edge habitats (Kapos, 1989; Zuidema et al., 1996) that have micro-environmental conditions that differ from those of interior habitats, such as more light availability and lower moisture. The implications of these changes could be dramatic for the conservation of the Gran Chaco native flora and fauna and, in particular, for "true forest species". For instance, edges could negatively affect the plant diversity of forests, promoting the decline of rare and specialized true forest species, as has already been observed in Chaco remnant patches (Cagnolo et al., 2006). Furthermore, edge effects may favor the invasion of exotic plant species (Torrella et al., 2013), alter plant reproduction and impair the regeneration of various species of the natural flora (Aguilar & Galetto, 2004; Aizen & Feisinger, 1994) and fauna (González, Salvo, & Valladares, 2014; Lopez de Casenave, Pelotto, Caziani, Mermoz, & Protomastro, 1998).

The trajectory of forest patch density (PD) showed specific temporal changes in the analyzed sectors and depicted a remarkable process of forest fragmentation over the last three decades. The significant drop in patch density over time observed in the NE sector, pinpoints a severe process of forest loss that has caused the forest patches to be on the brink of disappearing. Indeed, the presence of few small remnant forest patches is one of the most typical features of highly fragmented landscapes (Forman & Godron, 1986; McGarigal et al., 2005). In advanced stages of forest fragmentation many patches are completely removed, increasing isolation (Fahrig, 1997) and probably with dramatic consequences for biodiversity (Saura et al., 2014). In the NE sector, the ongoing fragmentation process does not depend on the breaking apart of forests, with a consequent rise in the number of patches (Riitters, Wickham, O'Neill, Jones, & Smith, 2000), but is due to a severe reduction of forest cover derived from the removal of whole patches (McGarigal et al., 2005). A similar process was observed in the first time step (1979–1999) of the NW sector where the significant decrease in patch density is related with a consistent reduction of forest cover and whole patches removal. Instead, the stable number of patches observed during the last time step (1999–2010) depicts a landscape where forest loss have occurred without the creation of new patches. In the W sector, the moderate increase of PD values during the first time span, describes a weak process of subdivision. Moreover, during the last decade, the accelerated process of forest loss have promoted the removal of many patches with the consequent diminution of PD values. Ecologically, the increase in the number (or density) of the forest patches, is primarily related to a process of subdivision in the former stages of fragmentation may have negative consequences on native biodiversity (see Fahrig, 2003 for a review). The stable number of patches depicts a transition between a landscape with few medium-sized forest patches to a more fragmented situation with a comparable number of smaller relict patches. In this case, the possible consequences on biodiversity could be trivial if compared to the effects of the habitat loss (Cushman et al., 2012; Fahrig, 1997; McGarigal et al., 2005). Finally, the drastic reduction in the number of patches, as that observed on the NE sector throughout the last three decades is related to forest disappearance in the advanced stages of forest fragmentation and could be clearly considered an important factor promoting negative effects on species richness and dispersal (Fahrig, 2003).

Last but not least, the combined effects of the progressive reduction in forest cover and the alteration of forest spatial pattern could promote local extinctions and lead to negative effects on various levels of the trophic network. In this way, fragmentation effects may disrupt basic ecological processes (Tilman, May, Lheman, & Novack, 1994). In relation to closed Chaco forest loss, previous studies have found lower values of plant species richness (particularly rare plants), which, together with edge effects, suggests a negative impact on native and animal-pollinated plants (Torrella et al., 2013).

5. Conclusions and conservation perspectives

The results of this study give rise to an important warning: the Gran Chaco has experienced both serious forest loss and spatial pattern changes, and such processes have been greatly exacerbated during the last decade. Furthermore in the NE sector, where the increase in annual precipitation made crop production possible and profitable, the high rate of forest loss (over the ~50%) and the abrupt changes of forest pattern are worrying evidences of closed forest extinction. Even in the western sectors, where logging is mainly related to the extraction of fire-wood and timber and to clearing for natural pastures, forests were strikingly fragmented. Our findings sound an alarm for researchers and stake-holders because exceeding a threshold of forest exploitation can lead to the irretrievable loss of biodiversity and function of the Chaco ecosystems.

The multitemporal overview of the presence and distribution of large and small patches with different spatial pattern characteristics in the Gran Chaco provides a sound framework to guide the development of an effective conservation strategy that includes fragments of varying sizes. This knowledge is particularly important because preserving larger fragments could promote the conservation of the overall biodiversity, but small fragments located in highly deforested landscapes could also play a role in the conservation of forest species (Piquer-Rodríguez et al., 2015). Distinguishing habitat spatial pattern changes from forest loss could have important implications for species conservation in Chaco forests where not all species are equally affected by habitat fragmentation. As for species threatened by forest loss (e.g. forest specialists), the solution is straightforward: habitat conservation and restoration (Fahrig, 2007), for species threatened by habitat isolation (e.g. intermediate dispersers, Tognelli, 2005), the problem appear less obvious as well as its solution. Probably one of the best management solutions is to connect up the 'broken apart' pieces of remaining closed forests by including new corridors or stepping stones (Piquer-Rodríguez et al., 2015; Saura et al., 2014). When, as in some sectors of the

Gran Chaco, forest extraction is severe and forest spatial pattern changes are relevant, both forest loss and isolation may seriously compromise the survival of the overall natural biodiversity (Bennett & Mulongoy, 2006; Fahrig, 1997; Hobbs, 2002). In such extremely fragmented landscapes, conservation efforts must concentrate on both, improving the condition of forest fragments (e.g., reintroduction of native species, removal of exotic species) in order to ensure their continued persistence, and enhancing the surrounding matrix including other natural cover types to reduce threatening processes (Hobbs, 2002). The last resort action is to reconstruct habitats using replanting and reintroduction techniques that guarantee the increment of both, available habitats for "true forest species" and connectivity (Saura & Rubio, 2010).

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Appendix A.

Trajectories of forests in the relationship space given by the % forest cover and the other fragmentation PIs (MPS: mean patch size (a), ED: edge density (b) and PD: patch density(c)). Light gray dots represent the observed values of pattern metrics in the entire set of sampled (10 × 10 km) grid units and symbols (squares, circles and triangles) indicate the arithmetic mean for each sector and date.

Appendix B.

Forest Pattern Indices (PIs) values in the West (W), Northwest (NW) and Northeast (NE) sectors for the years 1979, 1999 and 2010. PIs' arithmetic means, estimated from randomly sampled (10 km × 10 km) tiles, along with 95% confidence intervals obtained by a bootstrap procedure (BCa), are reported.

PIs	Sector	1979			1999			2010		
		Mean	Upper CI	Lower CI	Mean	Upper CI	Lower CI	Mean	Upper CI	Lower CI
% of forest	NE	20.27[a]	23.19	17.41	9.17[b]	11.77	6.61	1.49[c]	2.30	0.73
	NW	50.20[a]	56.07	44.57	47.89[a]	54.61	41.03	4.46[b]	6.54	2.59
	W	43.86[a]	49.92	37.63	30.54[b]	37.16	23.81	6.24[c]	7.84	4.67
Mean patch size	NE	5.60[a]	7.46	3.89	6.24[a]	8.49	4.14	0.37[b]	0.52	0.22
	NW	90.72[a]	153.70	33.27	73.25[a]	118.48	34.90	1.03[b]	1.35	0.74
	W	140.6[a]	208.88	74.86	47.46[a]	97.24	7.16	1.02[b]	1.25	0.83
Edge density	NE	51.41[a]	56.34	46.27	18.28[b]	22.73	14.07	5.90[c]	8.83	3.17
	NW	78.83[a]	85.25	72.27	69.23[a]	75.94	73.25	17.35[b]	23.15	11.71
	W	77.19[a]	82.49	71.94	61.64[b]	70.32	52.84	26.85[c]	32.68	20.99
Patch density	NE	4.96[a]	5.38	4.53	1.65[b]	1.97	1.33	1.16[b]	1.70	0.64
	NW	3.46[a]	4.20	2.74	2.48[ab]	3.02	1.95	3.22[b]	4.05	2.40
	W	3.41[a]	4.18	2.65	4.55[b]	5.18	3.93	5.28[b]	6.15	4.38

a, b, c, indicate significant differences on PIs arithmetic means between the compared data.

Appendix C. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.landurbplan.2015.08.006. These data include Google maps of the most important areas described in this article.

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