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A disappearing oasis in the semi-arid Chaco: Deficient palm regeneration and establishment

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ABSTRACT

Palm forests of *Copernicia alba* are a rare habitat in the semi-arid Chaco of Northwestern Argentina, are centres of high species diversity, and provide key resources for many species. Our goal was to assess the conservation status of five *C. alba* patches in Northwestern Argentina: Reserve; Embarcación; Palma Sola; Vinalito; and, Talar. We compared patches to identify the sites with greatest conservation needs based on four criteria: population size structure; palm density (of individuals with height >1.30 m); probability of seedlings being browsed; and, presence of potential seed dispersers. We found that three (Embarcación, Reserve, and Talar) out of five sites had palm densities greater than 200 individuals/ha and only one site (Embarcación) showed a reverse J-shaped size structure for height. Reserve and Embarcación had the greatest probability of seedlings being browsed (0.99 ± 0.01 and 0.88 ± 0.12, respectively). A total of 14 potential disperser species of mammals and birds were recorded across the five sites. Only Reserve harboured all of the potential dispersers, but at least two potential disperser species were recorded at the other sites. None of the palm patches studied had an adequate conservation status. However, Embarcación met three out of four criteria, and therefore it can be considered to have the best conservation status in the semi-arid Chaco. Palma Sola and Vinalito have the greatest conservation needs. To conserve *C. alba* in Northwestern Argentina, strategies are needed that ensure seedling establishment for future populations to reach an adequate density and structure.

Introduction

South America is a centre of palm (Arecaceae family) richness and diversity (Pintaud et al. 2008). Within the Arecaceae family, there are 200 palm genera known, with 1500 species that have thermocosmopolitan distribution (between 44°N and 44°S; Pintaud et al. 2008). Palm forests depend on water regulation by wetlands and their distribution is related to water availability (Bjorholm et al. 2005). Wetlands are one of the world's most threatened ecosystems as over-exploitation of natural resources and conversion to agricultural lands have already resulted in substantial loss and degradation (Sanchez-Carrillo & Angeler 2010). Wetlands in Argentina, and therefore palm forests, are seriously threatened by human activities, including drainage and use as water retention reservoirs or sinks for toxic substances (Neiff 2001).

Copernicia alba Morong. is a palm species distributed across the semi-arid Chaco ecoregion of South America. This ecoregion is expected to suffer the second highest rate of land transformation (after the Cerrado) to soybean monoculture (Dros 2004). In Argentina, the Chaco was the region with the highest rate of deforestation in the 90s (180,000 ha/y; i.e., −0.43% annual; Paruelo et al. 2005; Torrella et al. 2007). *C. alba* forms isolated patches intermixed with thorny shrubs and trees in the semi-arid Chaco (Cabral & Castro 2007). The species' distribution is determined by local water supply, which is particularly important in the semi-arid Chaco because patches are distributed in the scarce wetlands of this ecoregion. Patches harbour high species diversity of several taxa; *Copernicia alba* provides a key food resource for frugivorous species during the dry unfavourable season, and forests provide shelter and nesting sites for numerous mammals and birds (Beck 2005; Kahn & Arana 2008; Moraes 1991). Many of those mammals and birds could be key dispersers of *C. alba* seeds (e.g., *Rhea americana*), although seeds can also be dispersed by water (Moraes 1991; Poi de Neiff & Casco 2001). However, land cover and land use changes have reduced the extent and quality of palm patches and continue to threaten the conservation of the wetlands and many of the species that

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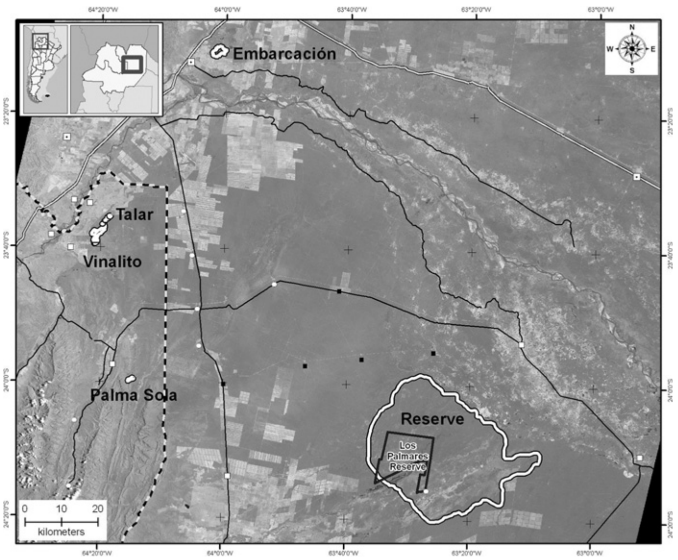

Fig. 1. Study area. Dashed line: provincial boundary. White line: palm patches. Black line: Los Palmares Flora and Fauna Provincial Reserve.

depend on these environments (Cristóbal 2006; Martínez Carretero 1995).

C. alba forests are often used as grazing land, which has resulted in additional impacts to palm forests in the Chaco. The structure of the forests has changed as the original herbaceous layer has been replaced by a woody stratum composed by *Prosopis ruscifolia* and *Geoffroea decorticans* (Torrella & Adamoli 2006). Cattle browse and trample *C. alba* seedlings (Moraes 1991). However, cattle have also been reported to disperse seeds of *C. alba* (Moraes 1991). With adequate management (e.g., reduction of stock density, rotations, or temporary exclusion), cattle raising could be less damaging to palm forests than land transformation (Báez & Jaurena 2000).

Despite the importance of palm patches in the semi-arid Chaco (Beck 2005; Kahn & Arana 2008; Moraes 1991) and the serious threats they face, there are no studies about the population status of *C. alba* in Argentina that we are aware of to guide conservation management strategies. Additionally, to ensure a functional connectivity between patches, knowledge of the native species that could be dispersers of *C. alba* seeds is needed (Beck 2005; Galetti et al. 2006; Taylor et al. 2006; Van der Wall et al. 2005). Our objectives were to assess regeneration and population status of *C. alba* and identify potential seed dispersers (mammals and birds) as a means to determine the conservation status of different palm forests and to identify those with the greatest conservation needs in the semi-arid Chaco of Northwestern Argentina (NWA).

Methods

Study site

The study was conducted in five palm patches of *C. alba* in the semi-arid Chaco (Fig. 1). Three palm patches were located in Jujuy province and two in Salta province. In Jujuy we worked in: (a) Palma Sola (23°59′46″S, 64°15′5″W; 69 ha), which belongs to a local resident who raises cattle; (b) Vinalito (23°39′9″S, 64°20′50″W; 79 ha), which is property of some Guarani original communities that raise cattle; and (c) Talar (23°39′6″S, 64°20′31″W; 656 ha), which is owned by Ledesma S.A.A.I. sugar cane company and is surrounded by a fence that excludes cattle. In Salta province, study sites were: (d) Los Palmares Flora and Fauna Provincial Reserve and buffer zone (hereafter Reserve; 24°12′S, 64°22′W; 108,393 ha), which is a protected area where local people live and raise cattle (Chalukian et al. 2002), and (e) Embarcación (23°11′24″S, 64°2′2″W; 635 ha), which belongs to private land-owners that raise cattle.

The climate across our study sites is continental with marked dry season and summer precipitation that range from 500 to 800 mm annually (Cabrera & Willink 1973). The average annual temperature is 20 to 23 °C (Cabrera & Willink 1973). The five palm patches have slopes of <5° (Nadir & Chafatinos 1990) and have a high probability of being transformed to agriculture or exotic pastures fields in the future, particularly those patches that are not currently included in the national or provincial protected area system.

Sampling design

From July 2009 to May 2010, we randomly established 57 plots that were 0.05 ha in area to survey palms >1.30 m height, and 59 plots that were 0.01 ha to survey seedlings. We varied the number of plots per site according to the size of the palm patch to ensure adequate sampling. In Reserve, we established 21 0.05 ha-plots and 21 0.01 ha-plots, in Embarcación 10 0.05 ha-plots and 10 0.01 ha-plots, in Palma Sola 11 0.05 ha-plots and 13 0.01 ha-plots, in Vinalito three 0.05 ha-plots, and three 0.01 ha-plots and in Talar 12 0.05 ha-plots and 12 0.01 ha-plots.

Palm density and population structure

We recorded the number of *C. alba* stems, the diameter at breast height (cm; DBH) and height (m) of all individuals with height >1.30 m in each 0.05 ha-plot to determine the palm density and size population structure at each site (Barot et al. 1999). We surveyed only individuals with height >1.30 m because palm trees have a leafless stem at this height. We compared palm density among sites using a generalised linear model (GLM) with a Poisson error distribution and a log link function because the response variable (palm density) represented counts. We conducted a posteriori tests of LSD Fisher to determine differences among sites, comparing random samples from independent populations (Di Rienzo et al. 2012; Quinn & Keough 2002).

To determine the population structure of palms in each site, we categorised the palms we measured into four height size classes: 1.3–5 m; 5–10 m; 10–15 m; and, 15–20 m (Cabrera & Wallace 2007). We considered DBH as an independent variable that influenced population structure because height and DBH were not strongly correlated ($R^2 = -0.31$, $P < 0.05$). We used the Kolmogorov maximum likelihood test to determine if the population size structure (height and DBH, analysed separately) at each site fit a bell-shape (normal) or a reverse J-shape (exponential) distribution (Di Rienzo et al. 2012). Additionally, we used generalised linear mixed models (GLMM) with a normal error distribution and an identity link function to compare the average palm height among sites, using plot as random factor and a posteriori LSD Fisher tests (Quinn & Keough 2002). We considered plot as a random factor to reduce type I error with the exception of palm and seedling densities, which were calculated at the plot level.

Regeneration

We recorded the number of *C. alba* seedlings in each 0.01 ha-plot to assess regeneration status at each site. Seedling density was calculated as number of seedlings per 0.01 ha-plot. To determine if *C. alba* seedlings were associated with different vegetation life forms we recorded the presence/absence of shrubs, trees, herbs, or grasses. We also measured the distance from each recorded seedling to the nearest tree and shrub, up to 250 cm (Batllori et al. 2009; García et al. 2000).

Data were analysed using GLMM, with a Poisson error distribution, a log link function, and plot as random factor (Quinn &

Keough 2002). We included site as explanatory variable to reduce type I error because differences between sites could be related to the surrounding vegetation. We tested for differences among sites using a posteriori LSD tests (Quinn & Keough 2002). We calculated Spearman's rank correlation coefficients to assess multicollinearity among independent variables, which indicated that correlation between variables was low (>0.60). To obtain the best model, we first selected the relevant variables with a manual backward stepwise procedure, removing insignificant ($P > 0.05$) variables at each step (Quinn & Keough 2002). We then used the Akaike Information Criterion (AIC; Di Rienzo et al. 2012) to decide the order of the variables to include in the model. To adjust the models we used "glmer" routine of lme4 package (Bates et al. 2011) of R implemented in Infostat (Di Rienzo et al. 2012).

We compared the average distance from between seedlings and the nearest tree and shrub among sites using a GLMM with a normal error distribution and an identity link function (Quinn & Keough 2002). We also performed GLMM to detect differences among sites on the association of seedlings to different vegetation life forms (Quinn & Keough 2002).

Browsed seedlings

We recorded the number of seedlings in each of the 0.01-ha plots that showed signs of browsing. We did not include Talar in our analysis because there were no browsed seedlings, nor Vinalito because there were no seedlings present. To assess if there was a relationship between surrounding vegetation and the probability of seedlings being browsed we performed GLMM analysis using a binomial error distribution (success = browsed seedlings and failure = non-browsed seedlings), a logit link function (Quinn & Keough 2002), and site as explanatory variable. We conducted a posteriori LSD tests (Quinn & Keough 2002) to determine if there were differences among sites in the probability of seedlings being browsed. To obtain the best model, we first selected the relevant variables with a manual backward stepwise, removing insignificant ($P > 0.05$) variables at each step (Quinn & Keough 2002). We then selected the best model using the Akaike Information Criterion (AIC; Di Rienzo et al. 2012).

Potential dispersers of C. alba

We collected all the feces of mammals and birds found ad libitum in trails, roads, and paths at each site and identified the species that consumed seeds of *C. alba*. We also inspected the feces to determine the number of intact *C. alba* seeds (Litvaitis et al. 1994). We report species detected directly or indirectly (i.e., through tracks or feces) at each site that could act as potential dispersers.

Conservation status

We assessed the conservation status of each site based on (1) the shape of the palm population size structure, assuming that bell-shaped structure indicates a lack of natural regeneration and reversed J-distribution indicates adequate regeneration and population sustainability (dos Reis et al. 2000; Ibarra-Manríquez & Mendoza 2003; Rosas et al. 1990); (2) palm density, assuming that >200 individuals/ha are required to ensure population viability of a palm patch (Molina Espinosa 2001); (3) probability of palm seedlings being browsed because browsing kills the seedling through the removal of the apical leaf bud (Moraes 1991); and, (4) presence of potential dispersers (Culot et al. 2011; Dracxler et al. 2011).

Results

Palm density and population structure

Palm density was significantly greatest in Embarcación (1132.00 ± 67.90 ind/ha), followed by Talar (426.67 ± 42.47 ind/ha), Reserve (240.95 ± 32.43 ind/ha), and Palma Sola (218.18 ± 30.96 ind/ha,) and significantly lower in Vinalito (133.33 ± 24.67 ind/ha; $P < 0.01$). The site with the highest palm height was Reserve (12.60 ± 0.69 m; $P < 0.01$). Embarcación (5.33 ± 1.00 m) had the lowest height; Palma Sola (10.32 ± 0.96 m), Vinalito (9.03 ± 2.24 m), and Talar (8.82 ± 0.92 m) were intermediate in height. Based on height, the population size structure at Embarcación had a reverse J-shaped distribution ($D = 0.06$, $P = 0.063$), whereas Palma Sola ($D = 0.09$, $P = 0.35$), Reserve ($D = 0.09$, $P = 0.062$), and Vinalito ($D = 0.14$, $P = 0.85$) showed a bell-shaped distribution (Fig. 2). Talar did not fit either distribution. Palm density in the smallest height class (1.3–5 m) was greatest in Embarcación, intermediate in Talar, and lowest in Reserve, Palma Sola, and Vinalito ($P < 0.01$; Fig. 2). We did not find any differences in palm density among sites for the other height classes.

Considering DBH size structure, all the sites fit a bell-shaped distribution ($P > 0.05$) except Talar, which did not fit any distribution shape (Fig. 2). In the two smallest DBH classes (10–20 and 20–30 cm), palm density in Embarcación was significantly higher ($P > 0.05$) than in the other sites. For the largest DBH class

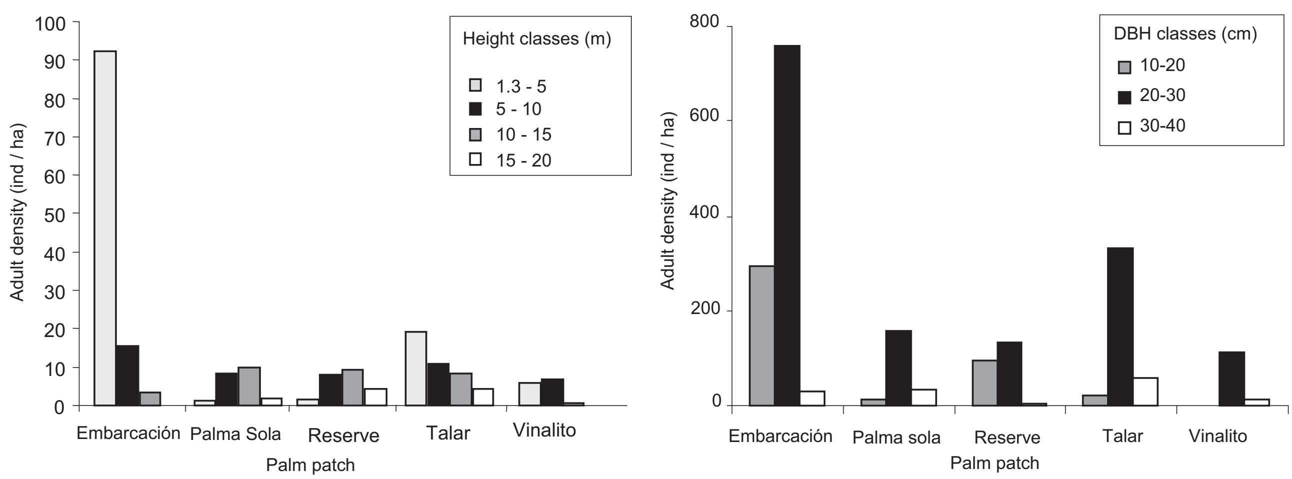

Fig. 2. Palm density of *Copernicia alba* by height (left) and DBH (right) classes found in five palm forests in Northwestern Argentina. Number of 0.05-ha plots surveyed in each site: Embarcación = 10; Palma Sola = 11; Reserve = 21; Talar = 12; and, Vinalito = 3.

Table 1
Coefficients (β), standard errors (SE), z value and significance (P) for each selected explicative variable of the multiple regression in five palm patches (i.e., site) in Northwestern Argentina. Response variable: Seedling density.

Variable	β	SE	z	P
Trees	0.04	0.0009	43.42	<0.01
Shrubs	−0.01	0.001	−10.22	<0.01
Distance to trees	−0.12	0.02	−6.39	<0.01
Distance to shrubs	−0.03	0.04	−0.84	<0.01
Site	5.67	0.24	24.03	<0.01

Table 2
Coefficients (β), standard errors (SE), z value and significance (P) for each selected explicative variable of the multiple regression in five palm patches (i.e., site) in Northwestern Argentina. Response variable:Percent of browsed seedlings.

Variable	β	SE	z	P
Trees	−0.03	0.85	−0.03	<0.01
Distance to trees	0.01	0.01	2.11	<0.01
Distance to shrubs	0.01	0.03	0.36	<0.01
Site	2.25	1.52	1.48	<0.01

(30–40 cm), palm density was significantly higher in Talar ($P > 0.05$) than in the other sites.

Regeneration

Across all sites, the average distance between *C. alba* seedlings and the nearest tree was 76.62 ± 10.78 cm, and 42.36 ± 7.17 cm to the nearest shrub. The majority (87%) of the trees closest to seedlings were *C. alba.* Seedling density was related to the presence of trees or shrubs, but not to the presence of grass or herbs (Table 1; $P > 0.05$). There were also significant differences between sites in seedling density associated with the presence of trees, which was highest in Reserve (866.52 ± 505.30 seedlings/ha), followed by Palma Sola (400.30 ± 233.32 seedlings/ha), Talar (45.12 ± 26.34 seedlings/ha), and Embarcación (43.27 ± 25.24 seedlings/ha; $P < 0.01$). There were, however, no significant differences in the seedling density associated with the presence of shrubs, herbs or grasses ($P > 0.05$).

There was a positive relationship between site and seedling density (Table 1). Seedling density was significantly greater in Palma Sola (1703.78 ± 13.61 ind/ha), followed by Reserve (745.98 ± 11.26 ind/ha), Talar (501.11 ± 10.47 ind/ha), Embarcación (403.23 ± 10.09 ind/ha), and Vinalito (no seedlings recorded; $P < 0.01$).

We found a negative relationship between seedling density per plot and distance to trees and to shrubs (Table 1). We did not detect significant differences among sites in the distance between seedlings and trees or shrubs ($P = 0.85$ and $P = 0.83$, respectively).

Browsed seedlings

The probability of seedlings being browsed was negatively related with the presence of trees ($P < 0.01$), but there was no relationship with the presence of grasses, herbs or shrubs ($P > 0.05$) (Table 2). Additionally, the probability of seedlings being browsed was positively related to the distance between seedlings and trees and seedlings and shrubs (Table 2). Site also had an effect on the probability of seedlings being browsed ($P < 0.01$; Table 2); probability was significantly greater in Reserve (0.99 ± 0.01) and Embarcación (0.88 ± 0.12) compared to Palma Sola (0.01 ± 0.01; $P < 0.01$).

Potential dispersers of C. alba

We detected feces of 14 species containing a total of 355 seeds of *C. alba*. Forty-two percent of the seeds were in pellets of *Ortalis canicollis*, 24% in *Pseudalopex gymnocercus* or *Cerdocyon thous*, 13% in *Bos taurus*, 8% in *Equus caballus*, and 13% in the pellets from other species (*Pecari tajacu*, *Tayassu pecari*, *R. americana*, *Puma concolor, Tolypeutes matacus, Mazama guazoubira, Felix* sp., *Zenaida auriculata* and other Columbidae). In Reserve, there was direct or indirect evidence of all 14 potential disperser species. We found evidence of fewer potential dispersers at the other sites, with six native (*P. concolor*, *P. gymnocercus*, *C. thous*, *O. canicollis* and an unknown Columbidae) and two exotic potential dispersers species (*B. taurus* and *E. caballus*) in Palma Sola, two native (*P. tajacu* and *M. guazoubira*) and two exotic potential dispersers species (*B. taurus* and *E. caballus*) in Embarcación, two native potential dispersers species (*M. guazoubira* and *R. americana*) in Talar, and two exotic potential dispersers species (*B. taurus* and *E. caballus*) in Vinalito.

Conservation status

None of the palm patches studied met all four conservation criteria (Table 3). We determined that the conservation status was highest in Embarcación, which met three of four.

Discussion

Our study suggests that *C. alba* patches in NWA could be threatened. Most sites had low palm density and a bell-shaped size distribution, which indicates that a high proportion of individuals in the population were intermediate in size based on height and DBH. The low number of small-sized individuals suggests that there may be factors preventing natural regeneration (Ibarra-Manríquez & Mendoza 2003; Rosas et al. 1990). Overgrazing, for example, might prevent establishment of *C. alba* if seedlings are trampled or browsed (Molina Espinosa 2001), which has been shown for other palm species (e.g., *B. capitata* [Molina Espinosa 2001; Rivas & Barilani 2004], *Neodypsis decaryi* [Ratsirarson et al. 1996], *Brahea aculeata* [Lopez-Toledo et al. 2011]). Additionally, other factors such as fires (Moraes 1991) or changes in the flooding regime (Chalukian et al. 2002) could also jeopardise *C. alba* regeneration.

The negative relationship found between seedling density and distance to shrubs may suggest that shrubs facilitate seedling development by providing improved growth conditions, including, for example, lower irradiance and reduced rates of evapotranspiration (Gómez-Aparicio et al. 2005). Additionally, the positive

Table 3
Conservation status and criteria for five palm patches (i.e., site) in Northwestern Argentina. −: poor; +: moderate; ++: good; +++: very good.

Site	Criteria				
	Population structure shape Height/DBH	Palm density	Probability of seedlings being browsed	Number of potential dispersers	Conservation status
Palma Sola	Bell/bell	−	0.01 ± 0.01	8	+
Vinalito	Bell/bell	−	No seedlings	2	−
Talar	No fitted	++	No browsed seedlings	2	++
Reserve	Bell/bell	+	0.99 ± 0.01	14	+
Embarcación	Reverse-J/bell	+++	0.88 ± 0.12	4	+++

relationship between the probability of seedlings being browsed and distance to shrubs suggest that shrubs may provide seedlings with protection from being browsed or trampled (Muller 1953) as it has been reported for several woody species with seedlings that are damaged more frequently by herbivores when they are not protected under shrubs (García et al. 2000; Gutiérrez & Squeo 2004). Moraes (1991) found a high density of seedlings around shrubs, suggesting that establishment of *C. alba* seedlings is improved by the protection provided by thorny woody species that reduce grazing and trampling of seedlings by cattle. Cattle might also be responsible for the negative relationship between the presence of shrubs and seedling density, as a reduction in the density of *C. alba* seedlings may favour shrub development (Morello & Saravia Toledo 1959; Torrella & Adamoli 2006).

Palma Sola had the highest seedling density and one of the lowest palm densities of individuals >1.30 m in height, with confidence intervals that included the 200 trees/ha threshold that ensures population viability (Molina Espinosa 2001). This suggests that although shrubs may act as nurseries for seedlings, the shrubs' crowns may ultimately inhibit seedling establishment, which has been shown for other woody species (García et al. 2000; Gutiérrez & Squeo 2004; Kitzberger et al. 2000).

Conservation status of palm forests

The palm patches that we studied show a poor conservation status. The size distribution of height and DBH for most of the patches was bell-shaped, indicating a lack of natural regeneration and establishment. Sites with livestock present had a high probability of the seedlings being browsed. Vinalito and Palma Sola were the smallest palm patches that we studied and in these sites palm population viability may be uncertain because palm densities were below 200 ind/ha (Molina Espinosa 2001). In other palm species (e.g., *Astrocaryum mexicanum*), patch size and palm density are negatively related (Arroyo Rodriguez et al. 2007). Moreover, the lack of seedlings and native potential dispersers suggests that Vinalito is the site with the worst conservation status. The low density of seedlings in Talar could also be related to the low number of potential dispersers recorded (Beckman & Muller-Landau 2007; Nathan & Muller-Landau 2000). Reserve is also likely at high risk, but the high number of potential dispersers and the implementation of the Reserve management plan might improve its conservation status in the future. Embarcación is the site at lowest risk based on our assessment, and conservation efforts must be taken to ensure maintenance of high palm density. We suggest developing management strategies that address cattle grazing as a means to improve regeneration of *C. alba*. Potential strategies include, for example, reducing cattle stocks to avoid overgrazing or rotating cattle to ensure that palms have an opportunity to overcome the height at which they are browsed or trampled (Teich et al. 2005).

To avoid functional isolation of palm patches, it may be necessary to ensure that native dispersers can move through patches (dos Reis et al. 2000; Galetti et al. 2006; Lindenmayer & Fischer 2006; Puechagut 2011). Considering that the Chaco is one of the ecoregions most threatened by fragmentation in Argentina (Paruelo et al. 2005), implementing ecological corridors that can maintain the connectivity among palm patches may be necessary (Baker 2011). Furthermore, for dispersers to fulfill their role, it might also be necessary to ensure adequate population numbers (Culot et al. 2011; Dracxler et al. 2011; Melo et al. 2009). It is unlikely that exotic dispersers can aid as long-distance dispersers because land-owners keep cattle within their property.

Our study is timely considering that Argentina is currently conducting its national forest land planning scheme. Information about the regeneration and population status is necessary to adequately categorise and prioritise palm forests and wetlands for management and conservation. Additionally, this work serves to establish a baseline on which to assess the sustainable uses (e.g., cattle grazing) of *C. alba* palm forests.

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