From pattern to process: estimating expansion rates of a forest tree species in a protected palm savanna

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RESEARCH ARTICLE

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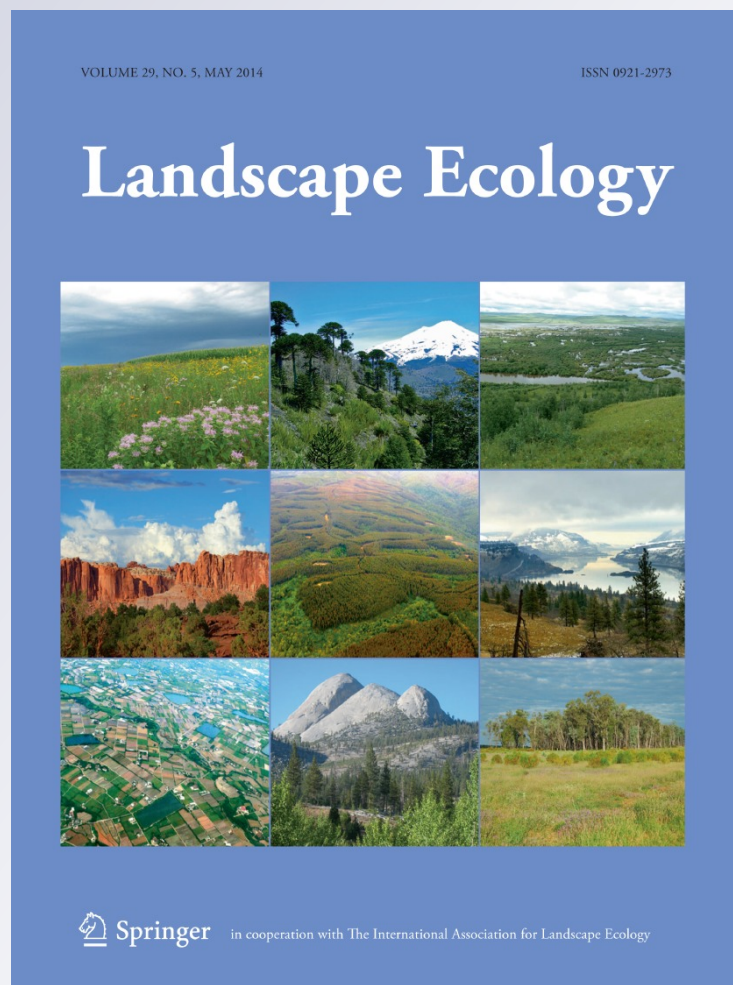
Andrés G. Rolhauser · William B. Batista

Abstract We assessed the possible influences of dominant tree density (*Butia yatay* palm trees) and fire on the expansion of a riparian tree population (*Myrcianthes cisplatensis*) over El Palmar National Park, a protected savanna in Argentina. Our approach is based on Skellam's model of population expansion, which predicts that populations with density-independent reproduction and random dispersal will exhibit Gaussian-shaped expansion fronts. Using Poisson regression, we fitted Gaussian curves to *Myrcianthes* density data collected at varying distances from a riparian forest, within four environmental conditions resulting from combinations of palm density (dense and sparse) and fire history (burned and unburned). Based on the estimated parameters, we derived statistics appropriate to compare attained expansion velocity, mean squared effective dispersal distance, and density-independent population growth among environmental conditions. We also analyzed the effects of palm density, fire history, and distance from the riparian forest on local maximum size of *Myrcianthes* individuals. Gaussian curves fitted the data reasonably well and slightly better than two alternative front models. Palm density and fire history interacted to control *Myrcianthes* spread, making unburned dense palm savannas the preferential avenue for *Myrcianthes* population expansion across the landscape. Limitation of *Myrcianthes* expansion by fire appeared to result from low survival of small individuals to fire, whereas facilitation of *Myrcianthes* expansion by palm trees may have resulted from increased population growth. Our results stress the interactive role of fire regime and local biotic influences in determining propagule pressure and tree establishment at the forefront, and the overall vulnerability of savannas to colonization by forest species.

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Introduction

Population expansions and contractions have occurred over millennia in association with natural environmental changes (Clark 1998; Hewitt 1999). Recent human-driven climate change and land-use modifications, however, have distorted such historical dynamics, seriously threatening species that cannot keep up with accelerated rates of environmental change, and boosting others that thrive under the new conditions (Neilson et al. 2005). Woody species expansion into grasslands and savannas is an example of such a distortion, where global- and landscape-scale factors interact to determine woody-species success (Scholes and Archer 1997; Bond 2008). In particular, humid grasslands and savannas have the climatic potential to develop into forests and are thus particularly sensitive to land-use changes that affect disturbance regimes (Scholes and Archer 1997; Bond et al. 2005). In turn, structural changes that result from the expansion of woody populations can severely modify ecosystem functioning and threaten the persistence of grasslands and savannas (Bond and Parr 2010). Hence, characterizing the patterns, rates, and controls of the expansion of woody populations in the landscape is a necessary step towards a comprehensive understanding of the dynamics of forest-savanna and -grassland boundaries (With 2002; Bond 2008). Studies of woody expansion have been mostly based on historical information provided by aerial photographs (e.g. Russell-Smith et al. 2004; Briggs et al. 2005). Here we infer woody-expansion rates by interpreting the current distribution of individuals at the landscape scale in terms of a classical mechanistic model of population expansion.

Mechanistic models state that the spatial spread of an expanding plant population depends on the rate of reproduction and the pattern of propagule dispersal (Higgins and Richardson 1996; Hastings et al. 2005). Combining these two, mechanistic models predict spatial patterns of population-density decay with distance from the origin, i.e. the population front (e.g. van den Bosch et al. 1992; Kot et al. 1996; Clark 1998). The first mechanistic model was developed by Skellam (1951) based on assumptions of density-independent reproduction (or population growth) and random, diffusive individual movements resulting in Gaussian-type dispersion kernels. Under these conditions, populations are predicted to approach a constant limiting velocity of expansion and to exhibit an expansion front with a Gaussian-type shape dependent on three parameters: initial density at the origin, mean squared displacement of individuals, and density-independent population growth rate (Skellam 1951; see also Turchin 1998). Therefore, if a Gaussian-like population front is recognizable in density-distance data (and provided some initial conditions are known), it is possible to approximate the average expansion velocity, dispersal distance and population growth, by acknowledging the relationship between these parameters and the shape of the front. This procedure is known as inverse modeling (or inverse approach), because model parameters that quantify processes are derived from observed data (e.g. Clark 1998).

In savanna landscapes, soil characteristics, fires, herbivores and dominant trees generate environmental heterogeneity that may affect reproduction and dispersal of expanding woody populations (Scholes and Archer 1997; Bond 2008). The direction of such effects depends on the particular species and demographic process. For example, depending on the susceptibility to fire and palatability of woody plants, fires and herbivores may either limit or promote their growth, development, and/or survival (Scholes and Archer 1997; Hoffmann et al. 2009). Scattered trees may promote woody plant establishment when they serve as perches for seed dispersers or as nurse plants for seedlings (Milton et al. 2007; Rolhauser et al. 2011). In contrast, dominant trees can also limit woody plant establishment through direct competition or enemy-mediated interactions (Chaneton et al. 2010; Rolhauser et al. 2011). As a consequence, specific responses of woody populations to biotic and abiotic environmental heterogeneity are likely to result in different pathways of encroachment at the landscape scale (With 2002).

In this paper, we investigate the population expansion of a native tree species in the palm savannas of El Palmar National Park, Argentina. Since 1965, El Palmar National Park has protected one of the few remaining populations of the palm tree *Butia yatay* (Mart.) Becc., along with its associated ecosystem (Ciccero and Balabusic 1994; Goveto 2006). Before 1965, land management in this area included cattle grazing and intentional fires, and the vegetation

largely consisted of a palm-tree layer of variable density and a herbaceous layer (Martinez Crovetto and Piccinini 1951). Tree species from riparian forests were not mentioned in historic floristic descriptions of *B. yatay* savannas (Lorentz 1878; Báez 1937; Martinez Crovetto and Piccinini 1951), and palms are the only trees visible in aerial photographs from 1965. As of 1970, cattle were completely excluded and fire control practices were introduced, although fires both natural and accidental have occurred over time (Ciccero and Balabusic 1994; Goveto 2006). Relatively large herbivores remaining in the Park after 1970, such as *Hydrochoerus hydrochaeris* L. (capybara) and *Lagostomus maximus* Desmarest (plains vizcacha), are rare and have restricted distributions (Ciccero and Balabusic 1994). This radical change in land use triggered a large increase of woody-species cover (Ciccero and Balabusic 1994; Goveto 2006). We focus on *Myrcianthes cisplatensis* (Cambess.) O. Berg (Myrtaceae), the most abundant tree species invading the savannas in the Park. *Myrcianthes cisplatensis* (hereafter named by genus), is a medium sized (15 m high), bird-dispersed tree living in the understory of the Paranaense Forest (Argentina, Paraguay and Brazil) and in riparian forests that extend southwards along the Paraná and Uruguay basins (Burkart and Bacigalupo 2005). In fire prone savannas, *Myrcianthes* trees are able to both resprout and reproduce vegetatively after fire.

The specific questions we here addressed were: (i) has the expansion of *Myrcianthes* proceeded from the riparian forests toward the uplands? (ii) What were the influences of palm density and fires on the expansion of *Myrcianthes*? To answer these questions we searched for population fronts (i.e. negative density-distance curves) of *Myrcianthes* over areas with contrasting fire histories and adult palm densities. We also examined the relationship between distance and local maximum basal diameter of *Myrcianthes* individuals, which should be negative for populations expanding over homogeneous environments. Finally, we interpreted the density-distance curves in terms of the pattern predicted by Skellam's model (i.e. a Gaussian population front). Applying inverse modeling, we derived statistics to compare approximate velocity of expansion, mean effective dispersal distance, and density-independent population growth among contrasting combinations of fire history and palm tree density.

Methods

Study system

El Palmar National Park (31°53′ S, 58°16′ W) extends over 8,500 hectares on the west margin of the Uruguay River, Argentina (Fig. 1). Mean annual precipitation is 1346 mm and mean annual temperature is 19 °C (Goveto 2006). Although rainfall is relatively concentrated in the warm season, high summer temperatures result in frequent water deficit and increased fire probability (Goveto 2006). Since 1970, several fires have burned large tracts in the Park while some areas have remained unburned (Goveto 2006). The landscape in the Park is organized by streams flowing toward the Uruguay River, among which El Palmar Creek has the largest watershed. In this watershed, the alluvial plain is occupied by riparian forests, while the highlands are occupied by savannas with various densities of *B. yatay* palms. In *B. yatay* savannas, topsoil is loamy-sand with about 85 % of sand.

Data collection

In 2005, we collected data on *Myrcianthes* density within an area of about 25 km² (Fig. 1). We delimited this study area so that the nearest tract of riparian forest to any potentially sampled patch was associated to the El Palmar Creek, and not to any other watercourse (Fig. 1). Within this area, we used a GIS to delimit all patches of at least 1 ha corresponding to each of the four environmental conditions defined as combinations of levels of two variables: density of adult palms (1–200 palms per ha, and 230–419 palms per ha) and time since last fire (>25, and <15 years). For each combination, we randomly selected two patches within each of five equally sized classes of distance to the riparian forest between 0 and 1.65 km, totalizing 40 patches. For simplicity, patches with low palm density (i.e. 1–200 per ha) are hereafter referred to as "sparse palm savannas", and those high palm density (i.e. 230–420 per ha) as "dense palm savannas". Further, patches with time since last fire <15 are referred to as "burned", whereas those with time since last fire >25 years as "unburned".

Between the fall and spring of 2005, in each of the 40 selected patches, we placed a 20 × 20 m² plot where we tallied all *Myrcianthes* individuals taller than 1 m and recorded their basal diameter.
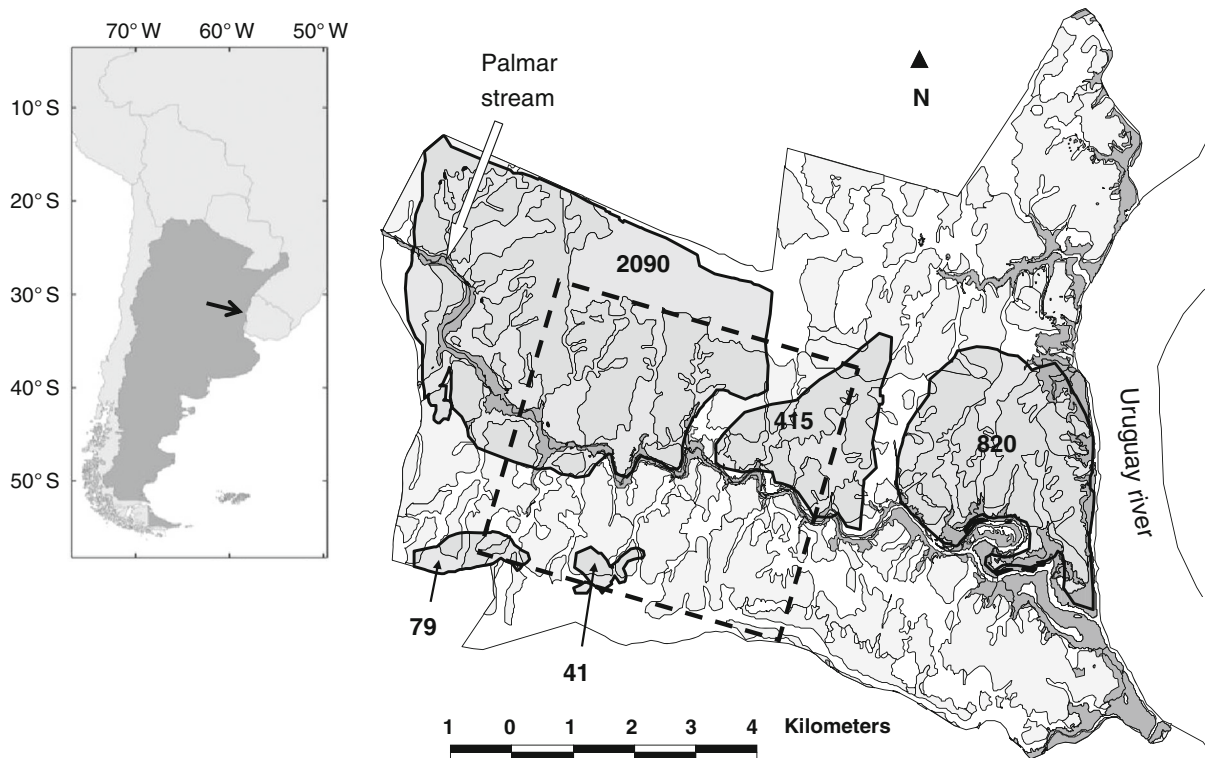
Fig. 1 Location and environment of El Palmar National Park. Riparian forests are shown in *dark gray*, landscape units containing adult palms in *light gray*, and other landscape units in *white*. The *shaded zones* represent areas having time since last fire <15 years in 2005; approximate areas in hectares are shown. The *discontinuous rectangle* delimits the sampling area

Individuals with multiple stems were assigned a surrogate basal diameter equal to the square root of the sum of squares of the basal diameters of all its stems (i.e. the diameter of a circular area that equals the total basal area of the individual; cf. Hoffmann et al. 2009). In addition, we recorded two covariates for each selected patch: shortest distance to the Uruguay River, and sand content of the topsoil, as determined with the hydrometer method on a sample from the first 15 cm (Robertson et al. 1999).

Pattern description

Tree density

For each of the four environmental conditions, we estimated a Gaussian shaped density-distance curve as expected from a population expanding according to Skellam's model. We performed this by fitting the following Poisson regression model to our data,

$$\begin{cases} n_{ijk}(x) \sim Poisson\left[\lambda_{ijk}(x)\right] \\ \ln\left[\lambda_{ijk}(x)\right] = \alpha_{ij} + \gamma'\mathbf{z}_{ijk} - \beta_{ij}\,x^2 \end{cases} \quad (1)$$

In the model, $n_{ijk}(x)$ is the number of *Myrcianthes* individuals in the k-th randomly selected plot with the i-th palm-density level and j-th time-since-fire level, located at a distance x from the nearest riparian forest, $\lambda_{ijk}(x)$ is the expected value of $n_{ijk}(x)$, $\mathbf{z}_{ijk}$ is the vector of covariates associated with the plot (distance to the Uruguay River and topsoil sand content), and α_{ij}, β_{ij}, and the elements of vector γ are model parameters (i, j = 1, 2). Parameters in vector γ represent the effects of covariates on the y-intercept for all four Gaussian curves. Parameters α_{ij} and β_{ij} code for the effects of palm-density and time-since-fire combinations on the y-intercept and the distance parameter of the corresponding Gaussian curve, respectively. Model fitting was performed by maximum likelihood using SAS Proc GENMOD (SAS Institute Inc. 1999). For the analysis, we

decomposed the α and the β coefficients in terms of contributions from palm-density level and time-since-fire level (see Appendix 1 in Supplementary Material), and we tested the parameters with Wald's method after correcting for overdispersion (Agresti 1996).

Note that if the frequency distributions of the covariates are homogeneous across distances from the nearest riparian forest, plugging in the mean vector of covariates gets the model to predict the logarithm of the geometric mean of $\lambda_{ijk}(x)$ across the variation of the covariates.

$$\ln\left[\tilde{\lambda}_{ij}(x)\right] = \alpha_{ij} + \gamma'\overline{\mathbf{z}}_{...} - \beta_{ij}x^2 \qquad (2)$$

By scaling the covariates so that they have zero mean ($\overline{\mathbf{z}}_{..} = 0$) we get,

$$\ln\left[\tilde{\lambda}_{ij.}(x)\right] = \alpha_{ij} - \beta_{ij}x^2 \qquad (3)$$

Tree size

We examined the relationship between maximum tree basal diameter and distance from the nearest riparian forest in each of the four environmental conditions using a normal linear regression model (Neter et al. 1992). We concentrated on maximum diameter to focus on pioneer trees and avoid effects of subsequent local dynamics. Maximum basal diameter was log-transformed prior to analysis, and predictor variables were as in model (1), except that distance x was not squared. We fitted the model by least squares and performed a standard analysis of variance. However, we did not test the effects in the model by comparing the ratios of mean squares with the F distribution as usual because the probability distribution of maximum tree diameters varies with the number of trees in each plot. We therefore performed a randomization test (Gotelli and Graves 1996). We assigned to each plot trees taken randomly and without replacement from the pooled set of all recorded trees; the number of assigned trees was equal to that observed in the plot. We repeated this procedure 10,000 times, performed the analysis of variance for each replication, and calculated the p-values as the proportions of the mean square ratios that were larger than the corresponding ratio in the original analysis.

Interpretation of the density-distance curves

Attained expansion

We used equation (3) to estimate the expansion attained since the beginning of the process in each environmental condition. We measured the attained expansion as the distance at which the geometric mean density equals 1 individual per plot. Ours was a problem of statistical calibration (see Osborne 1991), as we estimated an unknown level of a regressor (a distance x) corresponding to a certain mean value of the response variable (i.e. $\ln[\tilde{\lambda}_{ijk}(x)] = 0$). For the ij-th environmental condition our estimation of attained expansion was

$$v_{ij} = \sqrt{\frac{\alpha_{ij}}{\beta_{ij}}} \qquad (4)$$

Note that parameters v_{ij} are the x-intercepts of the log density-distance curves. We assumed that, at the time of sampling, the expansion process had occurred over the same period in all four environments (35 years, from 1970 to 2005). Under this assumption, comparison among the estimated v_{ij} provides a meaningful comparison of average expansion velocities. To statistically perform this comparison we used the following version of model (1) re-parameterized in terms of v_{ij},

$$\begin{cases} n_{ijk}(x) \sim Poisson\left[\lambda_{ijk}(x)\right] \\ \ln\left[\lambda_{ijk}(x)\right] = \gamma'\mathbf{z}_{ijk} - \beta_{ij}\left(x^2 - v_{ij}^2\right) \end{cases} \qquad (5)$$

to build confidence intervals for the estimated v_{ij} based on likelihood profiles as proposed by Williams (1986). We choose to use total distance instead of annual velocity to characterize the expansion process because the later carries uncertainty associated to the true elapsed time. Nevertheless, for a rough comparison with results in the literature, we used the time since cattle exclusion (35 years) to express our estimations as approximate mean annual velocities.

Dispersal distance and density-independent population growth

Under Skellaḿs model (1951), at any time t, the local density of individuals in an expanding population decreases with the distance from the origin as a

Gaussian curve specified by the following equation (in log form),

$$\ln[\lambda(x,t)] = r\,t + \ln[\lambda(0,0)] - \frac{\ln[\pi\,4\,D\,t]}{2} - \frac{x^2}{4\,D\,t} \tag{6}$$

where $\lambda(x,t)$ is the density at time t and distance x from the origin of the expansion, r is the density-independent per-capita population growth rate, and D is the diffusion coefficient which can be interpreted as the mean squared displacement of individuals by unit of time (cf. Turchin 1998). The diffusion coefficient is in fact related to the mean dispersal distance (m) as $D = \pi\ m^2/4t$ (see Appendix 2 in Supplementary Material). The pattern predicted by Eq. (6) holds both for a single-point origin in a one-dimensional space as well as for a line origin in a plane (Turchin 1998). The latter configuration fits our study case reasonably well, as riparian forests roughly stretch as a straight line across the sampled area (Fig. 1).

Note that Eq. (6) resembles Eq. (3) derived from our Poisson regression model as both are linear functions of the squared distance to the origin. Therefore, under the assumptions that all spread originated from source locations with the same density $\lambda(0,0)$, that the expansion time t has been the same for all four environmental conditions, and that each environmental condition is associated with unique values of D and r, we formulated approximations of these values by equating $\lambda(x,t)$ from Eq. (6) with the corresponding geometric mean $\tilde{\lambda}_{ij.}(x)$ estimated with our Poisson regression model (Eq. 3). The resulting approximations are,

$$D_{ij} = \left(4\beta_{ij}\,t\right)^{-1} \tag{7}$$

and,

$$r_{ij} = t^{-1}\left(\alpha_{ij} + \frac{\ln[\pi] - \ln[\beta_{ij}]}{2} - \ln[\lambda(0,0)]\right) \tag{8}$$

Estimation and statistical comparisons of the diffusion coefficients D_{ij} were obtained from the inverses of the estimated β_{ij} based on the invariance property of maximum-likelihood estimators. This property states that if $\hat{\theta}$ is the maximum-likelihood estimator of θ, then for any function $\tau(\theta)$, the maximum-likelihood estimator of $\tau(\theta)$ is $\tau(\hat{\theta})$ (Casella and Berger 2002). In contrast, the density-independent growth rates are not estimable from our data because the initial density $\lambda(0,0)$ is unknown. Therefore, we statistically compared the quantities,

$$r_{ij}\,t + \ln[\lambda(0,0)] = \alpha_{ij} + 0.5\left(\ln[\pi] - \ln[\beta_{ij}]\right) \tag{9}$$

among different environmental conditions. To execute the comparisons, we first used the Delta method to approximate the variance of the statistics $\hat{\alpha}_{ij} + 0.5\left(\ln[\pi] - \ln[\hat{\beta}_{ij}]\right)$, where the $\hat{\alpha}_{ij}$ and $\hat{\beta}_{ij}$ are the maximum likelihood estimators of the corresponding parameters. With the approximate variances, we built standard normal confidence intervals for $r_{ij}\ t + \ln[\lambda(0,0)]$. Under the assumption of a single density $\lambda(0,0)$ at the origin of spread over all areas, we interpreted the differences as estimated differences between population growth rates.

Caveat

Admittedly, the assumptions involved in our approximations to r and D imply overly simplified pictures of the landscape structure at El Palmar National Park and of the process of population expansion across it. First, areas with each environmental combination of palm-density level and time-since-fire are treated as continuous, and no migration of *Myrcianthes* among them is acknowledged. This assumption is not realistic because patches with high palm density are often interspersed within areas with low palm density. However, because migration between areas would blur the differences among them, any difference that is still detected with our data serves for comparison, at least qualitatively. Second, population expansion over each of these areas is assumed to have started from sources with equal density. This is a relatively safe assumption at least to the extent that systematic differences are not to be expected. Densities of *Myrcianthes* in the riparian forests before the expansion process would have been hardly affected by palm density in the neighboring savannas, and much less by fires that were to occur in the future. Third, within each environmental condition, frequency distributions of the covariate values are taken as homogeneous across distances from the origin of expansion. For sand content, this is at least a gross approximation as there is no striking soil-texture trend associated with distance to the riparian forests within 1.6 km from El Palmar Creek. With respect to the distance to the

Uruguay River, this assumption is quite reasonable, as expansion away from the El Palmar Creek is roughly parallel to the river.

As a matter of fact, it may be inexact to assume that the expansion of *Myrcianthes* over the landscape of El Palmar National Park occurs as a Skellam-type process, as diffusion is unlikely to realistically describe seed dispersal of this bird-dispersed species (cf. Kot et al. 1996; Clark 1998). Therefore, our estimations are not to be literally interpreted as referring to the values of the density-independent population growth rates and diffusion coefficients. Yet, provided a density-distance curve fits reasonably well to a Gaussian pattern, parameter r determines the average height of the curve [given $\lambda(0,0)$] reflecting total population growth attained at time t, and parameter D determines the spread of the curve which reflects the distribution of dispersal distances. Therefore, in this case, it is safe to interpret the comparisons of these parameters as rough indications of whether attained population growth and dispersal distances differ among the environmental conditions we regarded. As an additional check of the appropriateness of the Skellam's model in our case, we compared the fit of our *Myrcianthes* data to a Gaussian pattern with two additional front shapes: exponential and square root (see Appendix 2 in Supplementary Material).
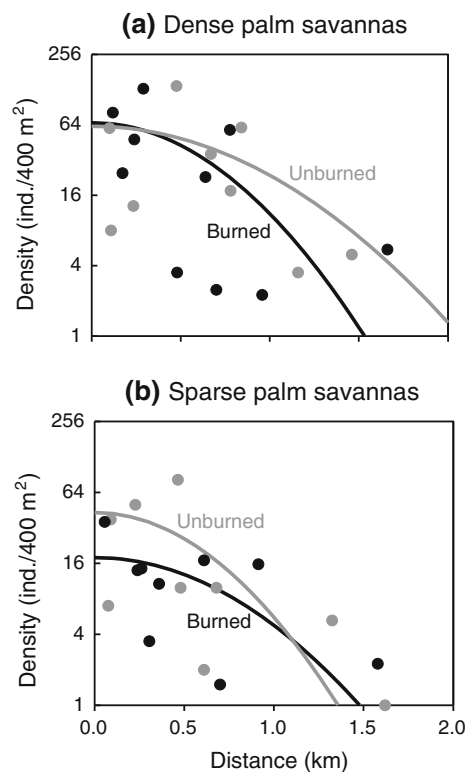
Results

Pattern description

Tree density

Average density of *Myrcianthes* decreased significantly with the squared distance to the nearest riparian forest (Table 1; Fig. 2). The Gaussian curves fitted the observed densities with substantial dispersion but with no noticeable systematic error (see Appendix 2 in Supplementary Material). Moreover, the goodness-of-fit of the Gaussian front was slightly better than those of the exponential and the square root fronts (see Appendix 2 in Supplementary Material). There was no significant density difference associated with distance to the Uruguay River or with topsoil sand content (Table 1). In addition, the estimated β coefficients did not differ significantly among environmental

Table 1 Type 3 analysis of the Poisson regression model fitted to density data of *Myrcianthes*

Source	DF	χ^2 value	p value
Palm density	1	3.896	0.048
Fire	1	0.854	0.355
Palm density × fire	1	1.123	0.289
Squared distance	1	13.410	<0.001
Squared distance × fire	1	0.002	0.963
Squared distance × palm density	1	0.071	0.790
Squared distance × fire × palm density	1	0.437	0.492
Distance to Uruguay	1	1.040	0.308
Topsoil sand	1	0.222	0.638

Fig. 2 Gaussian density-distance curves of *Myrcianthes* populations for four environmental conditions resulting from the combination of two levels of palm density [dense and sparse; panels (**a**) and (**b**) respectively] and two fire histories [time since last fire >25 years (unburned) and <15 years (burned); *black* and *gray* symbols respectively]. Curve parameters resulted from the analysis described in Table 1, and were calculated using the mean values of the covariates, distance to Uruguay River and topsoil sand, for all environmental conditions

Table 2 Type 3 analysis of a linear regression model fitted to individual basal diameter data of *Myrcianthes*

Source	Sum of Sq	DF	Mean-square ratio	*p* value
Intercept	9.58	1	24.81	0.936
Palm density	0.96	1	2.49	0.020
Fire	2.90	1	7.51	<0.001
Palm density × fire	0.44	1	1.14	0.126
Distance	1.93	1	4.99	0.029
Distance × palm density	0.25	1	0.64	0.544
distance × fire	0.07	1	0.19	0.587
Distance to Uruguay River	4.69	1	12.15	<0.001
Topsoil sand	1.07	1	2.78	0.294
Residuals	11.20	29		

Adjusted $R^2 = 0.63$. The effects in the model were tested on the base of 10,000 random data samples drawn under the assumption of homogeneous frequency distribution of tree sizes. The *p* values were calculated as the proportion of simulated mean square ratios that were greater than or equal to the corresponding ones calculated with the original data. The full model was simplified by removing the triple interaction ($F = 0.08$; DF = 1; $p = 0.962$)

conditions, as there were no significant effects of interactions of squared distance with palm density and/or time-since-fire detected in the analysis (Table 1). Estimated α coefficients did not differ significantly between burned and unburned sites, but they were significantly higher for environmental combinations corresponding to high than to low palm density (Table 1; Fig. 2).

Tree size

Maximum basal diameter of *Myrcianthes* (log-transformed) decreased significantly with increasing distance to the nearest riparian forest (Table 2; Fig. 3). However, as there were no significant effects of interactions of distance with palm density or with time-since-fire, decreases in mean maximum basal diameter with distance did not differ significantly among environmental conditions (Table 2). In addition, there were significant effects of palm density (positive), time-since-fire (positive), and distance to Uruguay River (negative) on the *y*-intercepts of the diameter-distance curves (Table 2; Fig. 3).
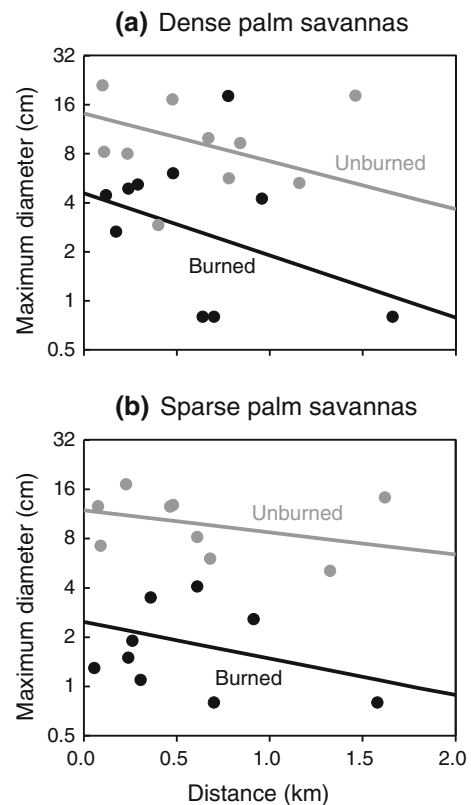
Fig. 3 Maximum basal diameter of *Myrcianthes* populations as a function of the distance from the nearest riparian forest for four environmental conditions resulting from the combination of two levels of palm density [dense and sparse; panels (**a**) and (**b**) respectively] and two fire histories [time since last fire >25 years (unburned) and <15 years (burned); *black* and *gray* symbols respectively]. Curve parameters resulted from the analysis described in Table 2, and were calculated using the mean values of the covariates, distance to Uruguay River and topsoil sand, for all environmental conditions

Interpretation of the density-distance curves

Attained expansion

Estimated expansion attained by *Myrcianthes* was significantly larger in areas with high palm density and >25 years since last fire than in any of the other three environmental conditions (Figs 2 and 4a). Also, attained expansion was significantly larger for high palm density and <15 years since last fire than for low palm density and >25 years since last fire (Figs 2 and 4a). Differences in attained expansion among environmental conditions were largely consistent across

front shapes (see Appendix 2 in Supplementary Material).

Dispersal distance and density-independent population growth

We detected no significant differences among environmental conditions in the estimated per-capita diffusion coefficients D_{ij} (Fig. 4b). Likewise, dispersal distances did not differ among environmental conditions for neither the exponential nor the square-root front (see Appendix 2 in Supplementary Material). We found significant differences in estimated $r_{ij}\ t + \ln[\lambda(0,0)]$ between dense and sparse palm savannas within fire histories (Fig. 4c). Under the assumption of equal initial density, these differences are interpreted as reflecting significantly higher per-capita population growth rate in dense than in sparse savannas within each fire history. In contrast, there were no significant differences in estimated $r_{ij}\ t + \ln[\lambda(0,0)]$ between fire histories within either palm density level (Fig. 4c). Patterns of population growth differences among environmental conditions derived from the exponential and square root models were qualitatively similar but subject to higher estimated error than those estimated under the assumptions of Skellam's model (see Appendix 2 in Supplementary Material).

Discussion

Myrcianthes population expansion from riparian forests

As of 2005, density of *Myrcianthes* at El Palmar National Park decreased with the squared distance to riparian forests associated to El Palmar Creek, a pattern consistent with the general prediction of Skellam's model of population expansion. Concomitantly, maximum basal diameter of *Myrcianthes* decreased with distance to El Palmar Creek, suggesting that trees are younger towards the forefront. Based on these facts, we suggest that the population of *Myrcianthes* has expanded over the landscape from the riparian forests, possibly since 1970, when cattle were completely excluded and fire control practices were introduced. This interpretation is consistent with studies pointing to disturbance regime modifications
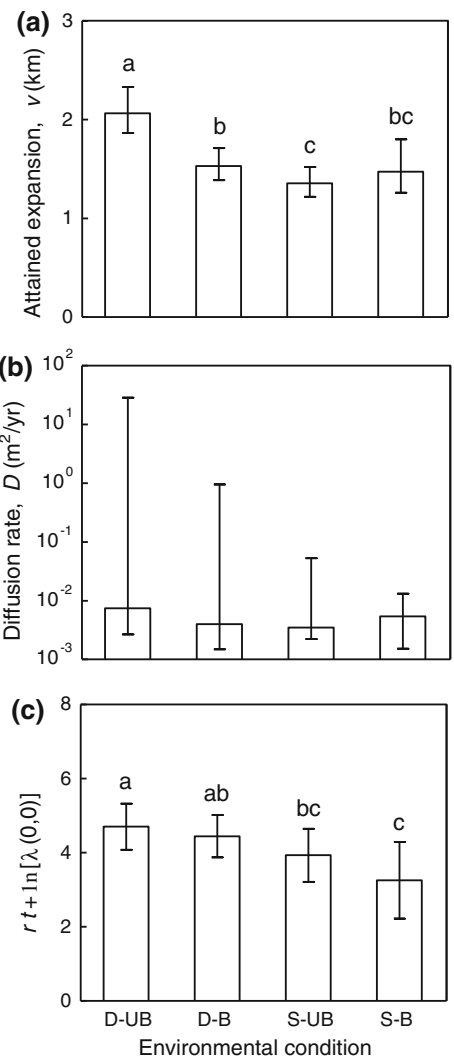
Fig. 4 Estimations of attained expansion (**a**), diffusion (**b**), and parameter $r\ t + \ln[\lambda(0,0)]$ (**c**) of *Myrcianthes* populations in four environmental conditions resulting from the combination of two levels of density of adult palms and two fire histories. Parameters correspond to a Gaussian-shaped expansion front. Parameter $r\ t + \ln[\lambda(0,0)]$ is used to approximate differences in density-independent population growth rate r among environmental conditions by assuming a unique value of initial density $\lambda(0,0)$ for all of them. *D* high palm density (dense palm savannas); *S* low palm density (sparse palm savannas); *B* time since last fire <15 years (burned); *UB* time since last fire >25 years (unburned). *Dispersion bars* are 95 % confidence intervals and *different lowercase letters above bars* indicate significant differences ($P < 0.05$)

as the factor triggering woody population expansion and encroachment over grasslands and savannas (Scholes and Archer 1997; Briggs et al. 2005; Bond 2008).

According to our estimations of attained expansion, the population of *Myrcianthes* had already reached the northern and southern edges of our study area (about 2 km away from riparian forests), at least in palm savannas not burned in the last 25 years. Assuming that the expansion process started in 1970 (35 years before our sampling), our estimates of attained spread would translate into average expansion velocities ranging between 38.7 m/year (in sparse, not recently burned palm savannas) and 59.0 m/year (in dense, not recently burned palm savannas). These values, however, should be regarded as maximal since it is conceivable that some *Myrcianthes* trees could have been present in palm savannas before 1970. Our estimations of expansion velocities fall within the range of expansion rates estimated for several populations of non-native trees and shrubs invading woody ecosystems and grasslands in other parts of the world (between 3.5 and 87.6 m/year, Pysek and Hulme 2005). In this context, our results suggest that the native species we studied could exhibit (maximal) expansion velocities comparable to those of similar non-native invading species.

The association of Skellam's model with Gaussian shaped population fronts was instrumental for deriving estimations of spread velocity, diffusion coefficients, and population growth rates from a two-parameter Poisson regression model. This fact implies that our estimations were based on two assumptions, whose possible consequences deserve consideration: density-independent population growth and a Gaussian dispersal kernel (see e.g. Turchin 1998). The first assumption was likely a reasonable approximation under the low local population densities we observed, as suggested by the lack of pattern in the residuals of the Poisson regression. The second assumption, in contrast, would be unrealistic as bird-dispersed species like *Myrcianthes* may exhibit exponential or fat-tailed dispersal kernels (see Willson 1993; Clark et al. 2005). In such cases, the Skellam model we applied would tend to underestimate population spread velocity (see e.g. Clark 1998). Yet, the Gaussian front fitted our data slightly better than both the exponential front and the square root (fat-tailed) front, while our main conclusions about the effects of palm density and fire history on *Myrcianthes* spread were by and large unaffected by the assumed shape of the advancing front (see Appendix 2 in Supplementary Material). The assumption of Gaussian dispersal appeared thus to

be a reasonable approximation for the relatively small spatial scale considered in our study (<2 km) (see also Pysek and Hulme 2005). Therefore, our estimations of maximal population spread of *Myrcianthes* would be conservative at worst, reinforcing our suggestion that this native species expanded as rapidly as invasive species do in other ecosystems.

Influence of palm density and fire on *Myrcianthes* population expansion

Our results indicate that palm density and fire history have interacted to control the expansion of *Myrcianthes* across the landscape (Fig. 5). In sparse palm savannas, we found no significant fire effects on *Myrcianthes* expansion velocity, mean effective dispersal distance, or density-independent population growth. In contrast, in dense palm savannas, the estimated distances attained by *Myrcianthes* expansion were significantly longer over unburned than over burned tracts. The difference observed, however, was not accounted for by statistically significant differences in either population growth or mean dispersal distance. This inconsistency is likely to result from the
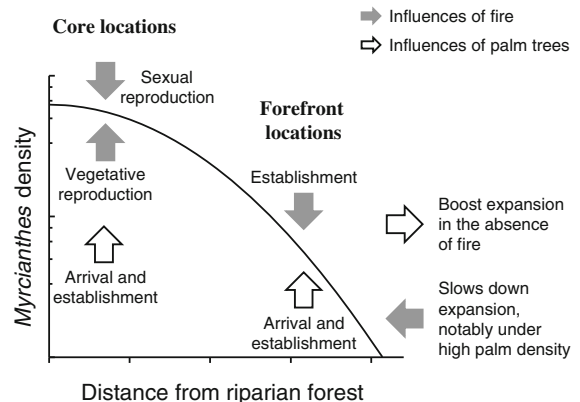
Fig. 5 Summary of inferred influences of fire and palms on the expansion of a native tree population (*Myrcianthes*) after cattle exclusion in a protected savanna in Argentina. The continuous line depicts a generic Gaussian-shaped population front (note density in log scale). Influences are represented by arrows, which either increase or decrease *Myrcianthes* local population growth (*vertical arrows*) or spatial expansion (*horizontal arrows*). *Gray arrows* represent the influences of fires and white arrows the influences of palms. Suggested demographic processes underlying the influences on *Myrcianthes* local population growth are written next to each *vertical arrow*. Local populations in the forefront are typically composed of trees smaller than those in core locations

fact that fire effects on tree stands can be twofold: on one hand, fires kill trees, on the other, they trigger vegetative reproduction of the top-killed but surviving individuals (Higgins et al. 2007; Bond 2008; Hoffmann et al. 2009). As survivorship to fires may be lower for newly established (smaller) than for mature, larger trees (Higgins et al. 2007; Bond 2008; Hoffmann et al. 2009), the net effect of fire on local population growth rate is likely to vary across the landscape depending on the age or size structure of the local populations. Our results show that local maximum sizes of *Myrcianthes* trees decreased with distance to the riparian forests and were significantly smaller in burned than in unburned savannas. Thus, in dense palm stands near the riparian forests, fires would have promoted active resprouting of mature trees rendering dense local populations composed of smaller and likely less fecund trees (Fig. 5). However, fires would have ultimately limited the expansion of *Myrcianthes* in the landscape by increasing the mortality of colonizing individuals in forefront locations (Fig. 5). We propose that, by shifting the balance from sexual to vegetative reproduction in local populations with mature trees, fires would have uncoupled to some extent population growth from seed production, and thus from population expansion across the landscape (cf. Higgins et al. 2007; Hoffmann et al. 2009).

Apparent effects of palm density on the expansion of *Myrcianthes* depended on fire history. In burned savannas, estimated population growth was significantly higher in dense palm stands, but this effect might have been overridden by fire-related mortality towards the expansion forefront, as we found no significant effects of palm density on *Myrcianthes* expansion velocity. In contrast, over savannas not affected by recent fires, both local population growth and spatial spread velocity of *Myrcianthes* were significantly larger under high than under low palm density. In addition, maximum sizes of *Myrcianthes* trees were significantly larger in dense than in sparse palm savannas. Palms are likely to boost *Myrcianthes* seed pressure both in sites near and far from the riparian forests by acting as attractive perching sites for dispersers (Rolhauser et al. 2011, see also Richardson et al. 2000; Milton et al. 2007). Further, the establishment and growth of *Myrcianthes* trees in dense palm groves might have been enhanced by nursing effects of palms possibly important during

frequent summer droughts, and/or by substrate conditions that might be correlated with high palm density (cf. Scholes and Archer 1997; Briggs et al. 2005). As the expansion proceeded, increased growth of *Myrcianthes* populations in dense palm groves not affected by fires top-killing the trees would have likely increased overall seed production and therefore seed pressure on forefront locations (Fig. 5). Based on the results presented here and elsewhere (Rolhauser et al. 2011), we suggest that the availability of perches and nursing plants may be a key biological control of palm savanna's vulnerability to colonization by *Myrcianthes*, and possibly by other native and non-native fleshy-fruited forest trees (cf. Milton et al. 2007).

The results discussed above can be placed in the conceptual framework of biological invasion studies that consider community invasibility and propagule pressure as drivers of invasion success (Williamson 1996; Lonsdale 1999). Within this framework, community invasibility is defined as the vulnerability of a community to invasion, while propagule pressure is the number of propagules arriving to a community (Williamson 1996; Lonsdale 1999). These two factors have often been treated in the literature as independent, invasibility as an intrinsic property of communities, and propagule pressure as an extrinsic force (e.g. Williamson 1996; Lonsdale 1999; Rouget and Richardson 2003; Davis et al. 2005; Catford et al. 2012). Here we note that community invasibility and propagule pressure can be interrelated when some intrinsic characteristics of the recipient community increase the odds of seed arrival (see also Eschtruth and Battles 2011). This seems to be the case of *Myrcianthes* and other colonizers (both native and exotic) that are dispersed by animals, whose behavior is highly affected by ecosystem properties (see e.g. Richardson et al. 2000; Wenny 2001).

Taken as a whole, our results agree with the notion that woody-population expansion over grasslands and savannas should be understood as the result of multiple interacting factors (Bond 2008; Chaneton et al. 2012; Hoffmann et al. 2012). Cattle exclusion and fire control practices at El Palmar National Park appear to have been the triggering factor for *Myrcianthes* expansion from the riparian forests into the *B. yatay* palm savannas. Seed dispersal by birds may have played a crucial role, allowing *Myrcianthes* individuals to reach savannas even with low availability of perches (see also Rolhauser et al. 2011).

Fires would have limited *Myrcianthes* expansion mainly by interrupting tree establishment at forefront locations and by shifting the balance from sexual to vegetative reproduction in older populations near the riparian forest. In contrast, in the absence of fire, palms would have boosted the process through the promotion of sexual reproduction, tree establishment and growth, and/or seed arrival. These mechanisms may be responsible for turning dense palm groves that remained unaffected by fire into the preferential avenue for *Myrcianthes* population expansion across the landscape of El Palmar National Park (Fig. 5). Our results thus stress the interactive role of disturbance regime and local biotic influences in determining propagule pressure and the overall vulnerability of savannas to colonization by forest species.

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