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The importance of fire refugia in the recolonization of a fire-sensitive conifer in northern Patagonia

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Abstract Seed dispersal and seedling establishment are essential for plant recolonization after disturbances, especially for plants that rely exclusively on sexual reproduction such as post-fire colonizer trees. Fire refugia may play a key role not only allowing trees to survive fire, but also functioning as seed sources after it. The estimation of seed dispersal and seedling establishment are essential for assessing plant recolonization ability, understanding landscape dynamics and determining which areas may not be able to recover due to lack of seed arrival. Here we study the post-fire recolonization ability of *Austrocedrus chilensis* (Cordilleran Cypress) from fire refugia in burned areas of northwest Patagonia, Argentina. We mapped all female trees, saplings and seedlings within and around fire refugia, recorded the reproductive capacity of female trees and characterized the microsite conditions for establishment. We used an inverse modelling approach and Approximate Bayesian Computation to estimate the seed dispersal kernel and the probability of seedling establishment. We found that the average dispersal distance of an *A. chilensis* seed was 88.52 m. The dispersal kernel was fat-tailed, meaning that *A. chilensis* has the capacity of producing accelerating expansions. Large woody debris, litter, and the protection of shrubs were the most important factors associated with the presence of recruits. We highlight the importance of fire refugia as seed sources for the recolonization of burned areas and thus the relevance of protecting these places to allow the persistence of fire-sensitive species.

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Introduction

Seed dispersal and seedling establishment are critical for plants, because they enable movement throughout the landscape, allowing for the recolonization of sites after disturbances (Ribbens et al. 1994; Clark et al. 1998a). This is particularly important for plants that do not have the capacity to resprout and depend exclusively on regeneration from seeds to recolonize the

landscape. Quantifying species recolonization ability, such as the probability of long-distance dispersal and the conditions which maximize establishment, is essential to understand plant population and community dynamics and to predict species expansion rates, especially within disturbed landscapes.

Post-fire colonizers are plants that do not resprout nor have seeds or fruits that survive fire, and thus, depend on seed dispersal from unburned remnants and subsequent establishment to recover after fires (Pausas and Keeley 2014). Accordingly, forest remnants are crucial for the recovery of burned landscapes composed of post-fire colonizer trees, and especially for those that are also fire-sensitive (i.e. plants that do not have any fire-resistant trait such as thick bark). This highlights the importance of fire refugia, that is, places that due to their biophysical attributes, such as the topographical setting and the composition of vegetation, are burned with lower severity or frequency than the surrounding landscape, thus allowing the persistence of forest remnants (Camp et al. 1997; Wood et al. 2011; Ouarmim et al. 2014; Krawchuk et al. 2016; Haire et al. 2017). In this way, fire refugia play a key role not only allowing post-fire colonizers fire-sensitive trees to survive fire, but also functioning as seed sources after it (Ordóñez et al. 2005; Kolden et al. 2012; Leonard et al. 2014; Krawchuk et al. 2016). Recently, some studies have assessed seed dispersal by quantifying regeneration patterns as a function of distance from forest remnants (Keeton and Franklin 2005; Kemp et al. 2016) or by assessing cone production of remnant trees (Ordóñez et al. 2005). Given the expected shortening of fire-free intervals and warmer conditions due to climate change, seed production and seedling establishment of post-fire colonizer fire-sensitive trees may be reduced (Enright et al. 2015). Thus, estimating these demographic processes is important to assess plant recolonization ability and to predict population dynamics and landscape recovery under changes in fire regimes.

The potential of fire refugia to act as seed sources and contribute in forest recovery might be assessed by estimating seed production and seed dispersal to the burned landscape. Seed dispersal capacity can be characterized by dispersal kernels, that is, mathematical functions describing the way seed dispersal probability changes with distance from a seed source (Clark et al. 1998a). Theoretical work has shown that (all else being equal) the shape of the dispersal kernel determines the rate of the population spread from a single source (Clark 1998; Clark et al. 1998a). A kernel with a tail that decreases exponentially or faster indicates that population spread is expected to occur at a constant rate and form an expansion front (Clark). However, a fat-tailed kernel (where the tail probability decreases slower than an exponential) implies that rare long-distance dispersal events are possible, allowing accelerating population spread as new sources in the landscape become established far from the original remnant (Clark 1998; Kot et al. 1996).

The arrival of seeds is a first step, but environmental conditions and seed-specific constraints determine the subsequent location of offspring (Nathan and Muller-Landau 2000). Successful establishment usually depends on microsite conditions, such as the type and depth of substrate, resource availability (e.g. light, water, nutrients), and may be modulated by biotic interactions such as predation or protection from adverse climatic conditions (Clark et al. 1998b; LePage et al. 2000). Thus, it is important to estimate these processes in post-fire colonizer fire-sensitive trees to assess their persistence and recovery capacity within burned landscapes.

Austrocedrus chilensis (Cordilleran Cypress) is a wind-dispersed post-fire colonizer conifer from northern Patagonia whose seed dispersal and establishment ability are crucial for its persistence and recolonization within fire-affected landscapes. The persistence of this endemic and fire-sensitive tree during the period of most extensive forest burning at the end of 19th century has been attributed to the existence of fire refugia (Veblen and Lorenz 1988; Landesmann et al. 2015). A recent palynological study found that *A. chilensis* may have expanded at average rates of 50–62 m per year during the Holocene (Souto et al. 2015). However, many empirical studies indicate that the seeds of this species usually disperse at < 20 m from the source, with the maximum distance recorded being between 40 and 60 m (Kitzberger 1994; Kitzberger and Veblen 1999; Rovere et al. 2005). Nevertheless, most of these results were obtained from observations from a single isolated mother plant or based on landscape change analyses. In any case, no study was designed to detect or quantify long-distance seed dispersal capability.

Here, we study the post-fire recolonization capacity of *A. chilensis* from fire refugia through the estimation of its seed dispersal kernel and the assessment of microsite conditions where recruits were found. We used an inverse modelling approach and Approximate Bayesian Computation, where we considered the reproductive capacity of female trees (i.e. seed sources), the spatial distribution of all mother plants and recruits, and the quantification of establishment probability related to microsite conditions (Ribbens et al. 1994; LePage et al. 2000; Schurr et al. 2008). Our study sheds light not only on the seed dispersal capacity of *A. chilensis*, but also on the probability of long-distance dispersal. Furthermore, it highlights the importance of considering fire refugia as seed sources within disturbed landscapes.

Methods

Study species

Austrocedrus chilensis (Cupressaceae) is a dioecious tree that typically reaches reproductive age at around 20 years (Brión et al. 1993; Nuñez and Rovere 2005). Wind pollination occurs during November. Female cones can be easily seen in the canopy of trees during summer and the beginning of autumn (mainly during February, March and April). Each female cone develops between two- and four-winged seeds which are wind-dispersed (Nuñez and Rovere 2005). Seed dispersal occurs during March and April, while germination can be observed after the winter season (Rovere et al. 2005). Seed production varies annually with some years displaying masting. Successful seedling establishment is usually associated with the presence of moist substrates and the protection by shrubs from direct sunlight and frosts (Gobbi and Schlichter 1998; Kitzberger et al. 2000; Letourneau et al. 2004; Nuñez et al. 2009). The seeds of *A. chilensis* do not remain viable in the soil for more than 1 year (Urretavizcaya and Defossé 2004).

Study site

Fieldwork was conducted in the austral summer of 2013 within the areas of Cerro Catedral and Lago Gutiérrez (near Bariloche city, Argentina) that were affected by fire in 1996 and in 1999, respectively

(Bran et al. 1996; Salguero 2000). Given that fire had occurred relatively recently, the areas are dominated by a dense and mixed shrubland composed of woody species which resprout rapidly after fire, such as *Nothofagus antarctica* (Nothofagaceae), *Discaria chacaye* (Rhamnaceae), *Schinus patagonicus* (Anacardiaceae), *Maytenus boaria* (Celastraceae), *Lomatia hirsuta* (Proteaceae) and *Chusquea culeou* (Poaceae). Within the burned area, *A. chilensis* individuals are present in very low abundance and are found only in the form of patches of surviving trees (i.e. remnants) and at the edge of the fire. *Nothofagus dombeyi* (Nothofagaceae), another tree species present in the burned area, is even less abundant than *A. chilensis* and is only present at the border of the fire.

The sampling was conducted in seven places identified as refugia in a previous study (Landesmann et al. 2015). These places are located in elevated topographic positions compared to the surrounding matrix and are characterized by a high rock-to-vegetation ratio which reduces fire severity allowing for the survival of fire-sensitive trees (Landesmann et al. 2015). Three refugia were found in the area of Cerro Catedral and four in Lago Gutiérrez. All of them supported *A. chilensis* trees that survived fire and included at least one female tree. Female trees were easily identified by the presence of cones in their canopy. Furthermore, 2013 was a mast seeding year (personal observation); therefore, all female trees presented an extraordinary number of cones in the canopy which made it even easier to identify them within the vegetation. This allowed us to locate all seed sources within the study area, which is a necessary condition to perform an inverse modelling approach (Ribbens et al. 1994).

Data collection

With the aim to estimate *A. chilensis* seed dispersal from refugia, in each refugium and the surrounding shrubland (hereafter referred to as "site") we mapped all *A. chilensis* female trees, saplings and seedlings. Adult female trees were located within the refugium and we delimited a minimum convex polygon which grouped together all female trees. Within the polygon we conducted a census to determine with a GPS ($\sim$ 10 m accuracy) the spatial location of all living adult trees, saplings, and seedlings (Figure A1, Online Resource 1). We considered adult trees as those that

presented cones in the canopy; saplings as those between 20 cm and 2 m height and without cones in their canopy and seedlings as those lower than 20 cm height. All seedlings and saplings are assumed to have regenerated after fire. We recorded sex and measured diameter at breast height (DBH) to all adult trees. For all female trees we also visually estimated the percentage of living canopy, which gives an indication of tree vitality and reproductive capacity. Given the xeric conditions of the refugia (associated with high rock cover, low soil moisture and high direct sunlight related to sparse vegetation cover; Landesmann et al. 2015), adult trees were frequently small in diameter and height, regardless of their age. Therefore, in the cases in which adult trees were about 2 m height, we measured basal diameter (BD) instead of DBH.

Given that the post-fire shrubland surrounding each refugium had an extremely dense vegetation structure that made searching for seedlings and saplings difficult, we established four 1 m wide × 30 m long radial transects starting from a different cardinal point from the edge of each female tree polygon (i.e. perpendicular to the polygon edge). Also, we established four 1 m wide × 60 m long transects disposed every 10 m perpendicularly to the radial transects (i.e. at 0, 10, 20 and 30 m from the polygon edge). Radial transects were 30 m long, but whenever we found a sapling or seedling in the more distanced perpendicular transect we established another one 10 m further from the previous one (i.e. at 40 m distance from the polygon edge) to keep looking for saplings and seedlings. This was repeated until no more sapling or seedlings were found in the more distant transect. Along each radial and perpendicular transect, we recorded with a GPS the spatial location of each sapling and seedling encountered.

To evaluate the relationship between microsite conditions and the presence of seedlings and saplings (hereafter referred to as "recruits") we recorded microsite attributes associated to every other recruit that we found in the polygons and the transects. Furthermore, to characterize microsite attributes associated to the absence of recruits, we randomly located 1 m² 124 control plots within the polygons and transects by choosing a random number from a list of coordinates. This made a total of 438 plots with data about presence–absence of recruits and presence–absence of microsite attributes. To characterize the microsite, we recorded substrate type (litter, ash,

rocks, and large woody debris such as bark and leaves bigger than 10 cm) and in the case of litter we also measured its depth. Ash was present in the site from the eruption of Puyehue-Cordón Caulle in 2011 (located at ∼ 100 km from the study site). Although some young seedlings may have been affected by ash deposition, we consider that its depth (1.6 cm in average) was not enough to produce a significant amount of seedling mortality. We also recorded the presence of trees, shrubs, herbs or branches, which may be functioning as protection from adverse climatic conditions or herbivory. We considered that the recruit was protected if it was located immediately under any of the protections mentioned above. In this case, we also measured protection's height.

Data analysis

Microsite conditions and the presence of recruits

To explore how microsite conditions were related to the presence of recruits we fitted a hierarchical logistic regression where site (i.e. each refugium and the surroundings) was considered as random effect. We also considered the effect of time since fire as we expected to find more recruits in the older fire (Cerro Catedral). Microsite substrate predictor variables included the presence–absence of litter, ash, large woody debris, and rocks. Litter depth was considered as a continuous variable. The explanatory variables associated to the protection of recruits were the presence–absence of trees, shrubs, herbs, branches, and lack of protection ("open sky"). We further included protection's height as another explanatory variable. After testing for multicollinearity, we excluded ash and protection's height, because they were highly correlated with other variables. Reference model variables were rocky substrate and lack of protection, given that this condition is usually the worst for *A. chilensis* seedling establishment. Therefore, we did not include these as explanatory variables, and accordingly, their importance is represented by the model intercept and the effect of each explanatory variable must be compared to this reference condition. The hierarchical logistic regression was fitted in R (R-Core-Team 2013) using Stan (Stan Development Team 2018) via the Rethinking package (McElreath 2015). We used weakly informative priors (Normal

with zero mean and unit standard deviation) for all coefficients and we tested for convergence before calculating posterior mean and 95% credible intervals.

Estimation of seed dispersal and establishment probability using inverse modelling

To estimate seed production and the probability function of seed dispersal distance (kernel) we followed an inverse modelling approach which has been developed to estimate dispersal based on patterns of seed arrival or established seedlings (See Ribbens et al. 1994; Canham and Uriarte 2006). For this, we first used the GPS coordinates to map each female tree and recruit within the polygon and the transects (Figure A1, Online Resource 1). Subsequently, for each site we made a grid with 1 m^2 cells which covered all the surveyed area (i.e. the polygon and transects) and each cell was considered as a "plot". We calculated the distance between all female trees and plots (irrespective of whether they had recruits). The expected seed arrival to each plot was modelled as the sum of the seed shadow of all female trees per site. That is, the expected number of seeds that reaches a plot "j" ($\widehat{s}_j$) was modelled as

$$\widehat{s}_j = \sum_{i=1}^{m} Q_i \times f\left(r_{ij}\right) \times A_j,$$

where the sum is made over all m female trees present in a site. The i-th female tree contributes Q_i seeds that arrive to the j plot with a probability given by the dispersal kernel f and according to the distance r_{ij} between female tree i and plot j and the area A of the plot (1 m^2). To model seed production we used a Poisson distribution with mean given by a linear function of basal area and scaled by the proportion of living canopy:

$$Q = b \times g \times v,$$

where b is a fecundity parameter that has to be estimated (because this parameter is unknown for *A. chilensis*), whereas g and v correspond to the basal area and the proportion of living canopy, respectively (Ribbens et al. 1994; Clark et al. 1999b). For the seed dispersal kernel, we used the 2Dt kernel (Clark et al. 1999b) because it has the ability to fit both short-distance and long-distance seed dispersal events (fat-tailed kernels). Kernel formula is

$$f(r) = \frac{p}{\pi u \left[1 + \frac{r^2}{u}\right]^{p+1}},$$

where p and u are the parameters of shape and scale, respectively. This kernel is similar to a Gaussian distribution when p tends to infinity and to a Cauchy distribution when p tends to zero.

Only a fraction of the seeds which arrive to a plot may have established successfully and survived until being observed during our fieldwork. Even though microsite conditions at the moment of sampling may differ from the conditions actually available at the moment of recruits' establishment, for this simulation we assumed that the microsite conditions were similar along the 14–17 years after fire and thus the establishment probability must be interpreted with this caveat. To estimate establishment probability, we used the variables shrub protection, large woody debris, and litter presence in the soil, which were the variables strongly associated to the presence of recruits according to the logistic regression described in the previous section (see results).

Parameter estimation using Approximate Bayesian Computation (ABC)

Approximate Bayesian Computation (ABC) is a means to obtain numerical samples that approximate the joint posterior distribution of a model by simulating data and comparing the simulated data with the observed data (Beaumont 2010; Hartig et al. 2011). In the simplest form of ABC, a large number of simulations are made using different combinations of parameters, which are obtained from the prior distributions of all parameters, and a similarity measure between simulated and observed data is computed for each combination of parameters. Then, a threshold in similarity between simulated and observed data is chosen to filter out parameter combinations. The sample of parameter values that pass this filter are used to estimate properties of the model posterior. The more restrictive the filter, the better the match between the approximate posteriors and those obtained by standard Bayesian analysis. Ultimately, ABC replaces the likelihood function that is usually employed in Bayesian analysis by a measure of distance or similarity between simulated and observed data. This approximation is useful when the likelihood function is difficult to calculate or it takes too much

computational time compared to the time that it takes to simulate the process that generates the data. In our case, some numerical instability appeared when we tried to estimate dispersal parameters using standard maximum likelihood or Bayesian methods. On the other hand, it was relatively easy to simulate seed production and dispersal from mother plants followed by seedling establishment, and to subsequently compare the quantity of recruits that appear in the plots with the observed data (the R script for parameter estimation using ABC is available in Online Resource 2).

Specifically, we first defined weakly informative priors for all model parameters, including those for seed dispersal, seed production, establishment, and survival probability. These priors comprise a range of reasonable values for all parameters. Subsequently, we simulated a million replicates of the seed production cycle, seed dispersal, recruit survival, and establishment. Each of these simulations (replicates) comprised 17 years for the refugia of Catedral and 14 years for Lago Gutiérrez refugia, considering the time since last fire of each area. For each replicate, we used a combination of parameters randomly sampled from the priors. Then, we compared the similarity between the simulated and observed data according to the sum of the log probabilities of the quantity of observed and simulated recruits within sampling plots and according to the total amount of simulated and observed recruits per site (see Online Resource 2). With this metric, we selected the 200 combinations of parameters which produced the set of simulated data that were more similar to the observed data. Our choice of 200 samples was a compromise between being restrictive about comparisons between simulated and actual data and having enough samples to estimate properties of the posteriors. With these values, we estimated the posterior mean and credible intervals for all parameters.

Results

We found a total of 1333 recruits within and around all fire refugia (571 saplings and 762 seedlings). The density of recruits was higher within Cerro Catedral sites, ranging between 0.05 and 0.16 individuals/m^2 on average, while Lago Gutiérrez sites had between 0.01 and 0.05 individuals/m^2 (Table 1). Recruits were located more frequently at < 50 m from mother plants, but they were also present between 50 and 150 m in all sites (Fig. 1). Indeed, in three of the study sites we found recruits between 150 and 200 m from a potential source. Regarding adult trees, there were more female trees than male trees within all sites, but both were generally more abundant within Cerro Catedral than in Lago Gutiérrez sites (Table 1).

Microsite conditions and the presence of recruits

Recruits were more frequently encountered in the older fire (Cerro Catedral) and were more likely to be found associated with large woody debris, litter, and under the protection of shrubs (Table 2). The largest effect on the presence of recruits was coarse woody debris, followed by time since fire, the presence of litter, and the presence of shrubs. For all the other variables considered, we did not find a consistent positive or negative effect (their 95% credible intervals included zero).

Seed production, seed dispersal, and establishment using inverse modelling

Using ABC and considering the average value of the posteriors ($u = 25,600$ m^2 and $p = 1.25$; Table 3, and Figure A2, Online Resource 1), we found that the average dispersal distance of an *A. chilensis* seed is 88.52 m (90% credible interval 33–140 m) from the mother plant (Fig. 2), whereas the median dispersal distance is 64 m (90% credible interval 20–105 m). The kernel shape parameter (p) was < 2, indicating a fat-tailed kernel (Clark et al. 1999b). According to this kernel, around 50% of the seeds fall at < 64 m from the mother plant, 95% arrive at < 250 m and 99% fall at < 450 m (Fig. 2). The estimated parameter of the reproductive capacity of an *A. chilensis* female tree (b) was 1198.8 seeds cm^2 yr^{-1} (Figure A2, Online Resource 1).

The parameters of establishment probability estimated by ABC were − 2.21 with shrub protection, 0.24 with large woody debris on the soil surface and 0.98 with litter in the soil (Table 3 and Figure A3, Online Resource 1). The highest establishment probability (0.23) occurred with litter or big woody debris as substrate, whereas shrub protection generated an establishment probability of 0.12. Without any protection and substrate, establishment probability was

Table 1 Number of female and male *A. chilensis* trees present at each site (refugium and surrounding shrubland)

Site	Female trees	Male trees	Recruits
Lago Gutiérrez 1	25	19	0.05 (0.03–0.07)
Lago Gutiérrez 2	9	7	0.01 (0.007–0.02)
Lago Gutiérrez 3	26	5	0.02 (0.01–0.03)
Lago Gutiérrez 4	20	5	0.04 (0.03–0.05)
Cerro Catedral 1	50	26	0.05 (0.04–0.06)
Cerro Catedral 2	34	22	0.13 (0.10–0.15)
Cerro Catedral 3	24	18	0.16 (0.13–0.18)

We also show the observed average density of recruits (ind/m^2) and the 95% quantiles intervals between brackets

Fig. 1 Frequency of distances (metres) between all female *A. chilensis* trees, saplings, and seedlings for the seven study sites. All distances were used in the estimation of the dispersal probability function (kernel). Each letter represents a different site, where **a** is Lago Gutiérrez 1, **b** Lago Gutiérrez 2, **c** Lago Gutiérrez 3, **d** Lago Gutiérrez 4, **e** Cerro Catedral 1, **f** Cerro Catedral 3, **g** Cerro Catedral 2 and **h** shows all sites combined
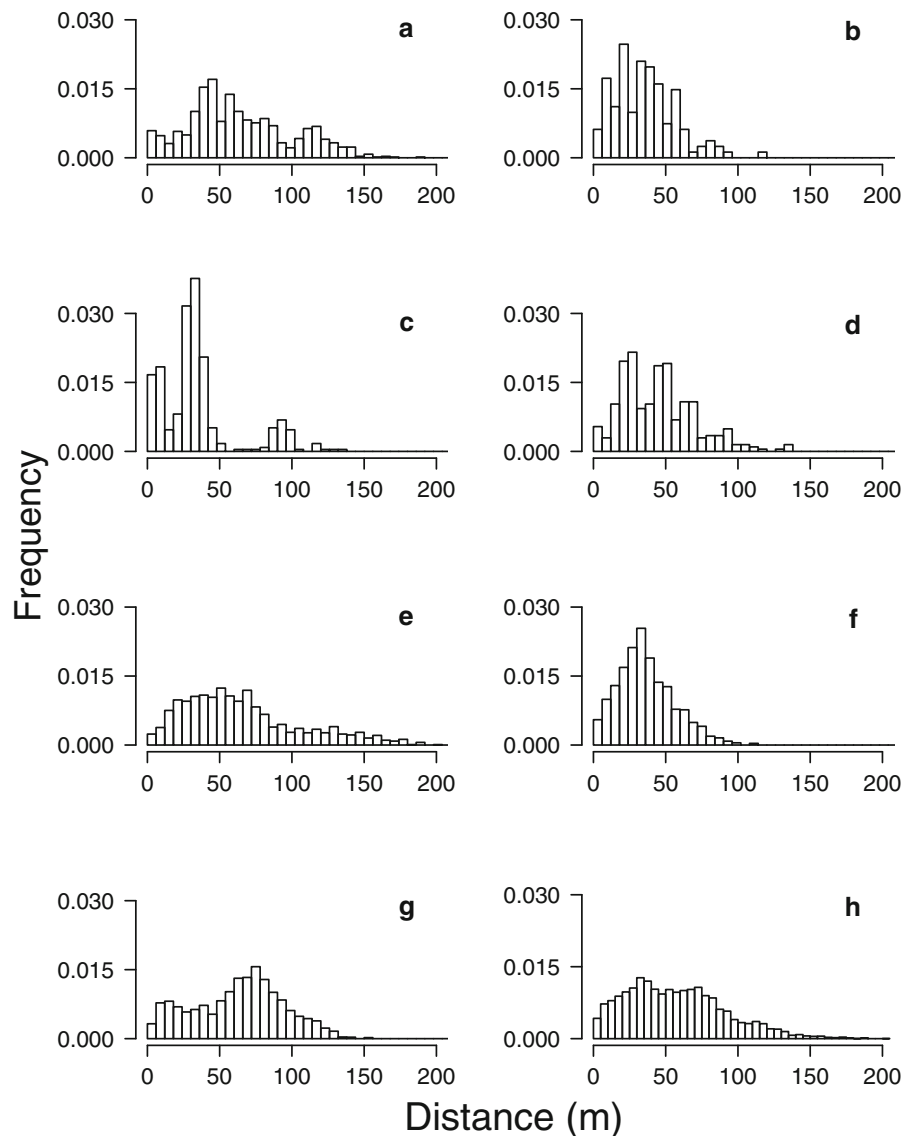
Table 2 Parameters estimates from the hierarchical logistic regression conducted to model the presence of recruits under different substrate conditions (large woody debris, litter, and litter depth), protection (shrub, tree herbs or branches) and time since fire

	Coefficient	Lower 0.95	Upper 0.95
Intercept	0.13	− 0.29	0.57
Litter depth	− 0.19	− 0.55	0.27
Large woody debris	**1.11**	**0.23**	**2.10**
Litter	**0.68**	**0.03**	**1.49**
Shrub	**0.67**	**0.17**	**1.28**
Tree	0.67	− 0.87	2.11
Herbs	− 0.01	− 0.65	0.64
Branches	0.15	− 1.22	1.07
Time since fire	**0.98**	**0.42**	**1.71**

We show the estimated mean posterior, and their 95% credible intervals. In bold we highlight those intervals that do not include zero

0.1. In contrast, when considering more than one factor, and in concordance with the logistic regression model, litter and large woody debris present in the soil generated the highest establishment probability (0.45). On the other hand, establishment probability was similar with shrub protection and litter or large woody debris in the soil (0.27).

Discussion

Fire refugia allow the persistence and recolonization of post-fire colonizer fire-sensitive trees and are key for the recovery of burned landscapes. In this study, we found that in northern Patagonia *A. chilensis* refugia are active seed dispersal sources that allow for post-fire forest recolonization. The average dispersal distance of an *A. chilensis* seed was estimated to be

88.52 m. The seed dispersal kernel presented a fat tail, meaning that *A. chilensis* has the capacity of producing accelerating expansions. The presence of large woody debris, litter, and shrub protection notably increased the probability of finding recruits compared to the predominant conditions of sparse vegetation and high rocky cover within refugia and recently burned areas (Landesmann et al. 2015).

Using inverse modelling we estimated that *A. chilensis* seed dispersal distance is much larger than previously thought. Preceding studies based on isolated trees or with other indirect methods, estimated average dispersal distances of 20 m and maximum of 40–60 m (Kitzberger and Veblen 1999; Rovere et al. 2005). This discrepancy may have to do with the estimation method as we considered both the reproductive capacity of female trees and the distance between all female trees and all recruits (Fig. 1). The inverse modelling approach that we used has been successfully applied to other wind-dispersed species. For example, for *Betula alleghaniensis*, mean seed dispersal distance was reported as > 60 m (Ribbens et al. 1994), and 38.4 m for *Pinus halepensis* (Nathan et al. 2001).
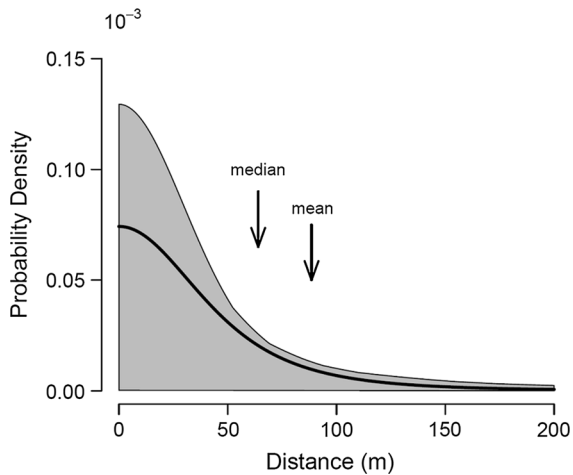
We found that *A. chilensis* seed dispersal kernel has a fat tail, as accounted by the estimated value of the shape parameter being < 2 (Clark et al. 1999b). Although the 90% credible interval included values up to 2.59, 80% of the posterior was < 2. Accordingly, even though half of the seeds may fall at < 64 m from the source, about 1% of them may fall at more than 425 m. This rather large seed dispersal distance value might be favoured by the higher topographic location of refugia which may increase seed dispersal distance given that seeds are released from greater heights compared to seed dispersal from more flattered parts of the landscape (Landesmann et al. 2015). Furthermore, secondary dispersal by for example wind, runoff

Table 3 Estimated parameters using ABC

	u	p	b	b0	b1	b2	b3
Average value	25600.17	1.25	1198.88	− 2.21	0.24	0.98	1.01
Lower limit	4354.51	0.01	48.37	− 4.33	− 0.36	0.27	0.42
Upper limit	47317.23	2.59	2634.39	− 0.03	1	1.93	1.59

We show the average posterior value and 90% credible interval (lower and upper limit) for the scale (*u*) and shape (*p*) dispersal kernel parameters; and for the female trees reproductive capacity parameter (*b*). We also show the average and the credible interval for the intercept (*b0*), presence of shrubs (*b1*), large woody debris (*b2*) and litter (*b3*) for the estimation of seedling establishment probability

Fig. 2 Estimated dispersal kernel of an *A. chilensis* seed from the mother plant (located at 0 m). The curve represents the kernel calculated by the posterior estimated value. The grey area represents the 90% credible interval estimated using Approximate Bayesian Computation. Arrows indicate estimated median and mean dispersal distance

and animals could also have influenced the final position of a seed or recruit as found in other systems (Schurr et al. 2005; Nathan 2006).

Long-distance seed dispersal events are usually important in explaining species recolonization after disturbances, especially for trees that reproduce only by seeds because it allows the formation of scattered points in the landscape that may function as new seed sources, allowing for accelerating expansion rates (Clark 1998; Nathan et al. 2002). In this way, after years of post-fire recolonization, forest remnants may be able to coalesce into continuous forests, unless a new fire event occurs. The accelerated expansion coupled with the capability to survive within refugia diminishes the dependence of post-fire colonizer trees to disperse from outside the burned area (because there are forest remnants within the burn), and thus, may be an advantage for the recolonization of large burned areas expected under climate change. This may explain the relatively fast *A. chilensis* forest expansion after the period of extensive fires in the end of 19th century in northern Patagonia (Veblen and Lorenz 1988; Kitzberger and Veblen 1999; Gowda et al. 2012) and supports its rapid expansion rate during the Holocene (Souto et al. 2015).

The presence of large woody debris was the most important factor associated with the occurrence of recruits. This pattern was obtained with both the

hierarchical logistic regression and ABC and may be explained because after fire there is scarce vegetation available to act as protection, but woody residuals such as bark, branches and fallen trees are abundant. Therefore, large woody debris may be acting as recruit protection during the first post-fire years. Similar results have been found on other tree species, like *Pinus pinaster* in Spain, where leaving logs or branches on the soil after fire highly improved seedling establishment through the reduction of direct solar radiation and temperature and the increase in soil humidity (Castro et al. 2011). Rocks, logs and standing tree trunks have also been reported to increase successful seedling establishment of *Pinus aristata* and *Pinus flexilis* after fire in the Rocky Mountains (Coop and Schoettle 2009).

In our study, litter in the soil and shrub protection were also associated with recruits' presence. This agrees with previous works that found that *A. chilensis* seedlings need protection from direct sunlight to successfully establish, especially during sub-optimal climatic years (Gobbi and Schlichter 1998; Kitzberger et al. 2000; Letourneau et al. 2004; Nuñez et al. 2009), and coincides with other studies that have proposed the use of nurse plants to restore degraded areas (Padilla and Pugnaire 2006). Microsites with litter in the soil, or a shrub canopy protection are better at retaining moisture and may present greater nutrient availability than open microsites (Gobbi and Schlichter 1998; Raffaele and Veblen 1998; Kitzberger et al. 2000). Indeed, it has been suggested that shrubs may also function as seed traps, and subsequently seeds may benefit from the better microsite conditions under the canopy (Rovere et al. 2005).

Our estimates of seed dispersal are based on the presence of already established recruits and assume that microsite conditions have not changed. Thus, we consider this work as a good first step towards the quantification of seed dispersal and establishment, but future studies should include seed trap data and establishment soon after fires. Another improvement would be to directly measure *A. chilensis* seed production. Furthermore, long-term studies are needed to assess how both seed production and establishment probability may vary annually, possibly associated with climatic variations (Clark et al. 1999a). Finally, assessing seed terminal velocity and wind speeds would allow for the development of mechanistic seed

dispersal models (Katul et al. 2005; Nathan et al. 2002, 2011).

Our study highlights the importance of forest fire refugia as they may function as post-disturbance seed sources and potential spread points within the landscape (Ordóñez et al. 2005; Kolden et al. 2012). Fire refugia contribute to the ecological memory of ecosystems conferring resilience to fire-disturbed landscapes (Johnstone et al. 2016). In this sense, these places are essential for the persistence and conservation of post-fire colonizers fire-sensitive taxa, considering the increasing concern about fire-sensitive trees immersed in a landscape of more frequent and severe fire events (Enright et al. 2015; Holz et al. 2015; Bowman et al. 2016). Accordingly, the study of fire refugia is gaining more attention and important efforts are being conducted to locate and characterize these places within fire-prone landscapes (Wood et al. 2011; Keppel and Wardell-Johnson 2012; Leonard et al. 2014; Landesmann et al. 2015; Krawchuk et al. 2016; Haire et al. 2017; Kolden et al. 2017). However, more studies are needed to estimate the actual role of fire refugia on the recovery of burned areas for which estimating demographic plant processes, such as seed production, dispersal and establishment is key. Understanding these processes is needed to model fire-sensitive species recolonization capability under scenarios of varying disturbance regimes, which would also allow to predict the rate of landscape recovery and to focus restoration efforts within the places where seeds are not capable to naturally arrive and establish.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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