



Spatial dynamics of expanding fragmented thermophilous forests on a Macaronesian island



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ABSTRACT

The increasing availability of aerial photographs and remote sensing images allows the forecasting of forest dynamics in response to land-use changes, such as the abandonment of rural activities. The cessation of these activities launches natural regeneration and demographic expansion of formerly fragmented and isolated forests. By tracking these changes over decades, we were able to identify the environmental factors that promote or hamper natural regeneration of forestlands disturbed for centuries. Here, we tracked the demographic expansion of *Juniperus turbinata* ssp. *canariensis* over a study period spanning six decades based on aerial pictures. We applied Local Indicators of Spatial Association (LISA) analyses to identify hotspots and coldspots of regeneration and we further quantified the role of ecological and anthropogenic factors in driving natural regeneration by applying a generalized lineal model. Aerial photos showed a clear demographic forest expansion during the approximately 60 years spanned by this study. LISA revealed that this regeneration was not homogeneous across the landscape; rather it was highly aggregated around an increasing number of hotspots of natural regeneration during the study period. The initial density of juniper individuals was the most important variable underpinning the demographic expansion followed by aspect, elevation, and distance to anthropic areas. According to our results, island juniper woodlands regenerate steadily in areas affected by moderate levels of anthropogenic disturbances. Our results provide highly valuable information to implement forest management plans. On-going and future conservation plans to recover the thermophilous Macaronesian forest will particularly benefit from this type of study.

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1. Introduction

Forest fragmentation and deforestation threaten forests by disrupting their functioning, thus compromising their potential for colonization and their persistence (Trumbore et al., 2015; Primack, 2002). Grazing and agriculture have severely affected formerly widespread forests inhabiting both continental or island managed landscapes (Trejo and Dirzo, 2000; Ribeiro et al., 2009; Caujapé-Castells et al., 2010). The study of the consequences of land use changes in anthropogenic landscapes is of utmost importance for confined territories that are highly impacted by human activities, such as many oceanic islands. However, we lack compelling, long-term data tracking the demographic expansion of remnant forest patches inhabiting abandoned rural areas, and this

hampers our understanding of the main factors underpinning the regeneration of threatened forests.

The use of aerial and satellite photographs has been proven to be an effective tool to study vegetation changes on large scales and over long periods, as opposed to traditional forest inventory methods (Davies et al., 2010). Aerial and satellite photographs serve as a source of data to quantify changes in the structure of vegetation over time at different spatial scales, such as cover and density variation in open canopy forests and semi-arid woodlands (Strand et al., 2006; Smith et al., 2008; Garzón-Lopez et al., 2012; García et al., 2014). They can also capture spatial patterns amenable to being described by spatial statistics, which are useful for testing competing hypothesis on the main processes driving natural regeneration (Pascarella et al., 2000; Pouliot et al., 2002; Kyncl et al., 2006), forest die-off (Breshears et al., 2005), or dispersal ability (García et al., 2014). For example, the spatial location of the vegetation gaps in a forest (i.e., sites with a very low density of

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plants) could be related to a strong seed dispersal limitation or to unsuitable conditions that hamper seed germination and establishment (Crawley and Ross, 1990). Previous studies based on aerial pictures in open-canopy forests have documented that aspect and elevation are important environmental variables influencing woodland regeneration (Johnson and Miller, 2006; Davies et al., 2010). Most of these studies have been conducted in extensive mainland areas, where environmental variables may be relatively homogeneous. However, few studies have been conducted on oceanic islands where many different environments can be found within a few kilometers and where the forests are confined to reduced areas across strong environmental gradients.

Of the open-canopy forests on islands that can be easily assessed via aerial photography, we chose the thermophilous forests native to the Canary Islands. They are located on the five western islands of the archipelago and have been highly impacted by human activities since the arrival of the first settlers (2500 BP) and the posterior Spanish colonization in the 15th century due to grazing, logging, and agriculture (Otto et al., 2010; Del Arco et al., 2010). Among others, juniper woodlands dominated by *Juniperus turbinata* ssp. *canariensis* are an important floristic element of the thermophilous forest on these islands. After centuries of exploitation, Del Arco et al. (2010) estimated that the current juniper woodland occupies approximately 3943 ha of the Canarian archipelago, unevenly distributed across the islands, with major populations located in La Gomera and El Hierro but also present in Tenerife, La Palma, and in small amounts in Gran Canaria. Macaronesian juniper woodlands are listed as a priority habitat in the European Union (9650 Endemic *Juniperus* forests) (Montesinos et al., 2009). Grazing and agricultural activities in the potential area of these forests greatly diminished after the 1950s (Rodríguez-Delgado and Marrero-Gómez, 1990; Arozena, 1991) favoring the local expansion of well-preserved juniper woodlands in recent decades. This natural regeneration offers us a unique opportunity to track the pace of forest expansion in a highly fragmented ecosystem and to identify the main ecological and anthropogenic factors underlying this expansion. Previous studies demonstrated that the recruitment success of this species is strongly driven by intra-specific nurse effects (Otto et al., 2010), and, therefore, we expected that successful regeneration would be driven by initial density (Crawley and Ross, 1990; Crawley, 2007).

Here, we used aerial photography to track the colonization pattern of a juniper woodland that has been expanding since the 1960s on La Gomera (Canary Islands). First, we estimated the tree density along a study chronosequence spanning six decades (1951–2012). Second, we identified hotspots and coldspots of regeneration by applying spatial statistics. We expected an uneven regeneration success due to the high ecological heterogeneity of the study site. Third, we assessed the relative importance of different ecological and anthropic factors influencing the population dynamics. We hypothesized that anthropic factors would have a significant effect hampering tree establishment, whereas the initial density would act as a main factor promoting regeneration. Finally, we propose some scientific-based guidelines to implement in ongoing and future management plans to recover the highly fragmented juniper forests across the Canarian archipelago (e.g., LIFE12 NAT/ES/000286 in Gran Canaria).

2. Materials and methods

2.1. Study species and study area

The genus *Juniperus* is comprised of more than 67 species (Abkenai et al., 2012). The Canary juniper is an endemic subspecies from the Canary and Madeira archipelagos (Otto et al., 2012; Jardim and Menezes de Sequeira, 2008; Acebes et al., 2010) related

to the species from the Mediterranean region, whose differentiation is today a topic of discussion (Adams et al., 2009). This species grows from the sea level to 500 m on the windward slopes and from 300 m to 1100 m on the leeward slopes (Otto et al., 2012), subject to precipitation rates between 200 and 500 mm (Fernández-Palacios et al., 2008). It has several dispersers on the islands, the most relevant being lizards from the *Gallotia* genus and birds, such as *Turdus merula* and *Corvus corax* (Fernández-Palacios et al., 2008). Crows are scarce on the archipelago according to Siverio et al., 2010. In addition, invasive mammals, such as rats (*Rattus rattus*) and the European rabbit (*Oryctolagus cuniculus*), can play a dual role as predators and dispersers for the *Juniperus* species (Mátrai et al., 1998; Schaffner et al., 2006; Fernández-Palacios et al., 2008; Suárez-Esteban et al., 2013a, 2013b).

The study area is located in Lomo de la Culata (28°11'32" N–17°15'7" W), Vallehermoso, on the northern slope of La Gomera (Fig. 1) in one of the oldest geological areas of the island (Carracedo, 2011). The area is very steep and rocky; however, it has better soil depth and climate conditions than other juniper woodlands stands in the archipelago (Otto et al., 2006). Its elevation ranges from sea level to approximately 500 m, with strong differences in vegetation within a few square kilometres, including halophilic species, such as *Euphorbia aphylla* and *Euphorbia balsamifera*, and uphill, hygrophilous species related to the humid laurel forests (*Erica arborea* and *Morella faya*). The woodland is classified within the island endemic association *Brachypodio arbusculae-Juniperetum canariensis* (Del Arco et al., 2006). There is also an area in which *J. turbinata* ssp. *canariensis* coexists with a plantation of *Pinus halepensis* that was run by ICONA (the no longer state-owned Institute for Conservation of Nature) in the 1970s (Arozena, 1991; Del Arco et al., 2006) but has been discarded.

2.2. Data collection

We selected the three best frames in the 64-year sequence of frames available for La Gomera: 1951, 1979, and 2012. Problems with shadow areas in the 1951 photography were remedied by using frames from 1956. Aerial photography from this year worked well in small specific areas but it was discarded as a whole due to some visualization problems. We assumed that the differences between 1951 and 1956 would not be problematic because of the slow growing rate of the species (Fernández-Palacios et al., 2008). All aerial pictures were obtained from the Ministerio de Defensa, Archivo Histórico Provincial de Santa Cruz de Tenerife and GRAFCAN. With these three photos, we generated three shape files in ArcMap (Environmental Systems Research Institute ArcGIS Desktop 9.3; Redlands, California, United States) with points representing all the recognizable individuals. It has been estimated, using field validation, that aerial photography can correctly differentiate *Juniperus* individuals with crowns from approximately 1.5 m in size. Shadows hampered visibility in some areas, and the progression of the introduced *Pinus halepensis* during the study period forced us to exclude other areas. We applied a contiguous grid composed of 50 × 50 m plots covering the entire study area to calculate the spatial density of the individuals. This was a suitable plot size because it fit within the existing small hillsides throughout the study area. We worked with a total of 589 plots for all the statistical analyses and therefore a total surface area of 1.47 km².

2.3. Spatio-temporal dynamics

2.3.1. Univariate and bivariate indices of autocorrelation

We first explored the spatio-temporal patterns of covariation in density among neighboring plots by testing the clustering from the aggregation of plots with similar or dissimilar density values. To do this, we estimated Moran's I index, a global spatial autocorrelation

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