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Elevational and structural shifts in the treeline of an oceanic island (Tenerife, Canary Islands) in the context of global warming

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ABSTRACT

Global warming is changing the structure and elevational limits of treelines around the world. This could become a threat particularly on islands, where usually high mountain ecosystems occupy small areas. Tenerife, with a maximum elevation of 3715 m, is an excellent example of this. In this subtropical island, the treeline composed by endemic pine forests is expected to go up in elevation due to global warming, invading the summit scrub ecosystem. However, there is a lack of knowledge about shifts and trends of the island treeline from a multi-temporal perspective and how invasive herbivores are influencing these changes. In this study, we evaluated the past and current state of the *Pinus canariensis* treeline on the southern areas of Tenerife, where natural forests persist, and an increase in temperature due to global warming has been already detected in the last decades. For that purpose, we counted the number of pine trees in aerial photographs for the years 1963, 1987 and 2016 and performed generalized additive models to evaluate the role of the different macro-variables involved in the regeneration processes. Complementarily, we performed ten transects to evaluate current forest structure and the influence of invasive herbivores (rabbits and mouflons) from 1600 m to the upper limits (2400 m). Our results reveal an increase in tree density and slow but consistent advance of the treeline in this part of the island during the last 53 years. Interestingly, positive relationships were found between number of trees and temperature. On the contrary, negative correlation was detected between seedlings and saplings and herbivores, a factor that is influencing the forests structure at all elevation levels. Our results show the importance of the herbivore control to ensure a healthy forest structure that allow an adequate migratory capacity of the species with the global warming.

1. Introduction

Globally, treeline elevational limits have been changing during last century mainly due to a combination of global warming and the cessation of uncontrolled deforestation (Holtmeier and Broll, 2005; Harsch et al., 2009). Treeline ecotone is usually characterized by limiting factors such as extreme temperatures, desiccation or absence of “safe sites” for recruitment (Battlori et al., 2009; Berdanier, 2010), so climate change is pointed out as a softening process of many of these aspects, facilitating in most cases recruitment, increase in density or advance of the treeline in elevation (Grace et al., 2002; Kullman, 2007; Harsch et al., 2009; Liang et al., 2011). However, while advances in elevation are clearly occurring in many temperate and cold alpine areas (Jobbágy and Jackson, 2000; Grace et al., 2002; Danby and Hik, 2007; Holtmeier and Broll, 2010), trends are not so clear for subtropical and island treelines. In these areas, droughts can be the key factor limiting growth and recruitment (Jonnson et al., 2002; Morales et al., 2004; López et al., 2013; Irl et al., 2015). In many oceanic islands, those droughts are related to the subsidence inversion of trade wind, which combined with immature soils and absence of well-adapted species to high mountain environment explain, in most of the cases, that their treelines are usually located around 1000–2000 m lower than in the continent at the same latitude (Leuschner, 1996; Holtmeier, 2009; Berdanier, 2010; Irl et al., 2015).

This is the case of the treeline in the Canary Islands, where the limit of the forest can be easily distinguished in the highest islands of the archipelago, La Palma and Tenerife, which exceed the 2000 m above sea level. In our days, the treeline in these islands is composed by only

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one endemic tree species, *Pinus canariensis* Sweet ex Spreng., although, several authors have pointed out that an upper treeline with open stands of the currently rare *Juniperus cedrus* could exist above 2000 m (Del Arco et al., 2006; Nogales et al., 2014). *Pinus canariensis* can be naturally found in these islands from 300 m up to 2400 m, being more frequent between 850–1800 m (Blanco et al., 1989; Del Arco et al., 1992; Del Arco and Rodríguez, 2018).

These elevational limits are expected to fluctuate, as a remarkable increase in temperatures in the last decades has been detected for this archipelago. That increase is being more important in the areas above 600 m due to a lesser tempering effect of the sea, but especially above 2000 m (Martín et al., 2012; Luque et al., 2014). As a consequence, a displacement in elevation of the current bioclimatic belts can occur, affecting also to those typical of the pine forest (Del Arco, 2008; Del Arco and Garzón-Machado, 2012; Del Arco and Rodríguez, 2018). Trends are not so clear for precipitation and the location of the subsidence inversion, but expectations seem to point to a slightly more arid scenario (Sperling et al., 2004; Martín et al., 2015). Tenerife is the island with the wider elevational range of the archipelago, up to 3715 m in the stratovolcano Teide, so most of the studies on this topic have focused on this island. However, the most complete study until date about the Tenerife treeline structure (Šrůtek et al., 2002), was only performed on a very specific area of the northern slope where, besides the climatic limitations, geological factors are considerably constraining expansion. In base to that study, the treeline of Tenerife was defined as stable on Harsch et al. (2009). Other studies, focused on a dendrochronological or ecophysiological point of view, have concluded that *Pinus canariensis* has several environmental difficulties to continue advancing beyond the current treeline due to drought and damage by frost (Jonnson et al., 2002; Köhler et al., 2006; Luis et al., 2007). Also strong winds have been pointed out as a cause of the deformation of pine individuals in these areas (Hollermann, 1978).

However, any of these previous studies have considered the use of remote sensing imagery to analyze the shifts in the treeline of Tenerife from a multi-temporal perspective, which could reveal different trends to what has been suggested until date. Aerial photographs have demonstrated to be very useful to assess shifts in the treeline ecotone in relation to global warming for many studies in the last decades (i.e. Gehrig-Fasel et al., 2007; Coop and Givnish, 2007). These photos currently span a long period in the Canary Islands, as they are available since the 50–60 s, so we are able to detect shifts on the treeline of Tenerife in the last decades.

The aim of this study is to evaluate the shifts of *Pinus canariensis* treeline in Tenerife in the context of the recent global warming and spanning the maximum period possible with aerial pictures. Our hypothesis is that advances are occurring in certain sectors of the island, being climate variables combined with human impacts cessation key factors, while at the same time invasive herbivores are limiting that expansion.

2. Materials and methods

2.1. Study area and study species

We focused our study on Tenerife island, which contains the wider continuous elevational gradient of the Canarian archipelago and holds some of the most extensive pine forests of these islands. As our goal was to determine which environmental factors are influencing elevational changes of *Pinus canariensis* in the treeline ecotone, we selected the most preserved areas of this ecosystem, which are located in the southern slope of Tenerife (especially in Vilaflor but also some areas of Arico, see Fig. 1), according to historical data (Del Arco et al., 1992; Quirantes et al., 2011) and a preliminary field and remote sensing study. All the study area corresponded to the Natura 2000 protected areas of Corona Forestal Natural Park and Teide National Park (declared natural reserves in 1994 and 1954 respectively). Logging activity and livestock are not permitted, but two invasive herbivores are still present: the European rabbit (*Oryctolagus cuniculus*) and mouflons (*Ovis orientalis*) (Rodríguez-Luengo, 1993; Cubas et al., 2017). We tried to avoid working directly on plantations or recent burned areas. Only one large fire partially affected our study area in 1998 (specifically in the Vilaflor locality).

These forests are characterized by occupying a broad range of soils (Blanco et al., 1989; Morales et al., 2005) and tend to be present in a

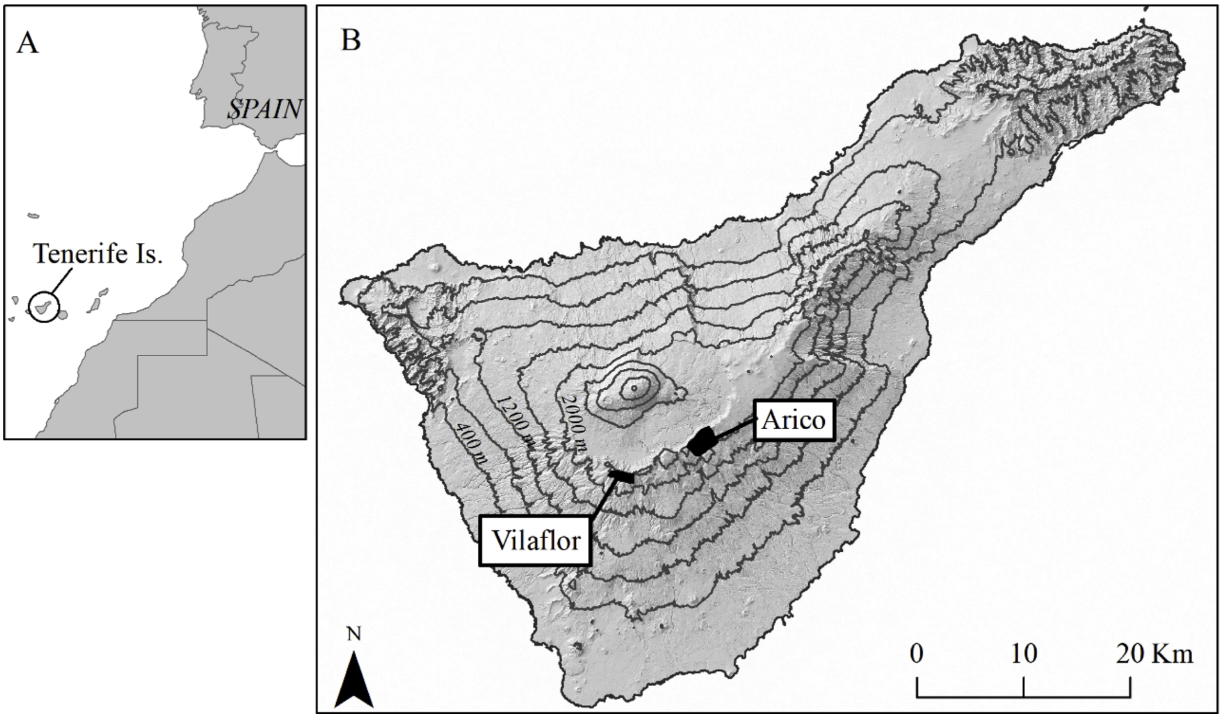

Fig. 1. Localization map of Tenerife island (A) and study locations (B).

wider altitudinal range in the leeward slopes, where they do not have to compete with the laurel forest associated to the NE trade winds (Del Arco et al., 1992). Climatologically, *Pinus canariensis* has an optimal distribution in areas of more than 750 mm of annual precipitation and a mean annual temperature of 13 °C (Blanco et al., 1989). However, it can withstand extreme conditions such as an annual precipitation of 250–300 mm or temperatures of −13 °C due to its high plasticity (Morales et al., 2005; Luis et al., 2007; Barbour et al., 2012). All these characteristics make this species partially tolerant to the harsh environmental factors that are present in the summit ecosystem of this archipelago.

2.2. Sampling methods

We divided our work in two complementary approaches using remote sensing analyses and a selection of plots for forest structure analyses. For the remote sensing analysis, we used aerial photographs corresponding to 1963, 1987 and 2016 in two areas (Vilaflor and Arico) above 1900 m. We used them to assess, at a landscape scale, the changes observed at the treeline spanning comparable periods of 24 and 29 years between each pair of photographs, and a total of 53 years for the whole period. We obtained these photographs from GRAFCAN (2018) (https://www.grafcan.es/, accessed in March 2018), being two of them (1987 and 2016) already ortho-rectified when acquired, while the 1963 picture had to be ortho-rectified using the georeferencing tool in ESRI ArcMap 10.1. The resolution of the three photographs was comparable, ranging 25–40 cm/pixel. To avoid common errors produced by automatic classification of images, such as considering shadows as individuals in the old photos, we counted the number of pine individuals in these areas. For that purpose, we created for the three photographs a vector layer in ESRI ArcMap 10.1, manually assigning a point to each pine individual (see Fig. 2). We considered only those individuals that in each case had enough size to be easily recognizable as pines. They usually had a crown diameter greater than 1.5 m or presented the typical pointy shadow of the species in its first stages. To count the number of pines, we first divided the study area in a continuous grid of plots of 50 × 50 m (covering a total of 4.57 km^2), assigning a count of pines for each plot. Secondly, to relate environmental macrovariables to the changes that we observed in the number of individuals through the pictures, we obtained data of elevation, aspect and slope from a digital elevation model and calculated the distance of each plot to areas affected by recent fires to assess their possible influence in the regeneration processes. Finally, we obtained for each cell the following climatic variables: mean annual temperature (T_{ann}), minimum temperature of the coldest month (T_{min}), maximum temperature of the warmest month (T_{max}), annual precipitation (P_{ann}), precipitation of the driest period (P_{dry}) and precipitation of the wettest period (P_{wet}). The maps for these variables have a resolution of 50 × 50 m, and they were obtained from the public data repository of the project 'Clima Impacto' developed by Santana and Martín (2013). All the data is derived from local meteorological stations, from which the authors have generalized the information to the entire island through regressions. We also considered two lithological categorical variables simplifying the Geological Map of the Canary Islands (Instituto Geológico y Minero de España and GRAFCAN, 2010) according to the type of materials (loose deposits or solid lava flows) and composition (silicon or basalt rocks).

The current forest structure was analyzed along 10 transects located in preserved pine stands along elevational gradients (adapting the method of Juntunen et al., 2002). At each transect four well-differentiated zones were selected in which random plots were performed: montane forest, timberline, treeline and isolated trees areas. At the lowest elevation (1600–2000 m), the montane forest stands allowed us to know how is the forest structure in this ecosystem in its optimal development areas. The timberline (2000–2200 m), was considered as the area where the montane forest ends in terms of density, with the last old growth pine individuals and maintaining still continuity of the canopy cover. That limit was visually estimated using aerial photography. The treeline (2200–2400 m) was defined as the last continuous line with tree individuals. After that line, we worked with isolated individuals, which were located between 2200 and 2500 m. In each one of these four zones three subplots of 30 x 30 m were established, reaching a total of 120.

At each plot, height, diameter at breast height (DBH), diameter at 20 cm height (D_{20}) and two perpendicular crown diameters were measured for each pine individual. For seedlings, only height and two perpendicular side diameters were measured. Then, all individuals were classified into height classes. As it is expected to be more individuals in the lower size classes, especially at higher elevations, and plants under 70–100 cm have strong herbivore effects (Cooke and McPhee, 2007; Meinzer et al., 2011), the first eight classes from seedling to 2 m were classified in ranks of 25 cm. After 2 m, individuals were classified into classes of 2–5 m, 5–10 m, 10–20 m, 20–40 m and above 40 m, reaching a total of 13 height classes. To assess the potential effect of rabbits and mouflons, we assigned to each plot an abundance value following Cooke et al. (2008). This scale ranges from 0 to 5 depending in the amount of pellets found in the area of study and the distance in which they are grouped. Complementarily, we noted the number of individuals with apparent herbivory damages such as cuts or marks on the stems.

2.3. Statistical analysis

2.3.1. Remote sensing analysis

As our data was not normally distributed, we performed generalized additive models (GAM) in R Studio 1.0.136 to have a better understanding about the role of all the variables involved in the regeneration processes of the spanned chronosequence. We used as dependent variables both, density of pine individuals per plot for the populations of 1987 (D_{1987}) and 2016 (D_{2016}). As predictors, we used all the environmental variables described before and the number of individuals from the immediately previous photograph (D_{1963} and D_{1987}

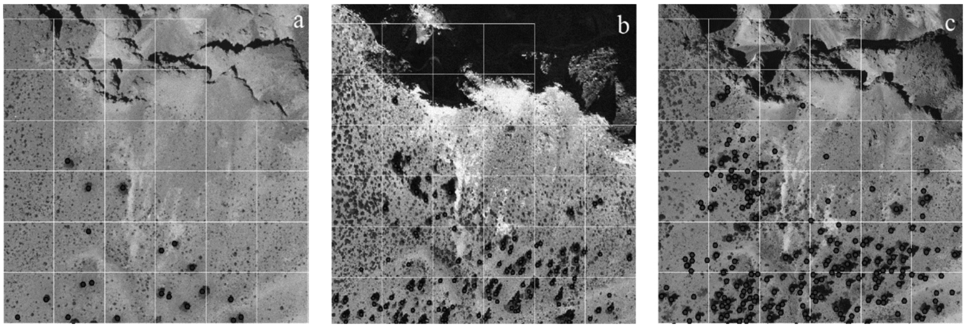

Fig. 2. Example of an area of the treeline in Vilaflor in (a) 1963, (b) 1987 and (c) 2016, showing the 50 x 50 m grid and the pine individuals as black points.

respectively). To perform these models, we avoided collinearity by excluding variables strongly correlated ($R^2 > 0.5$), through a preliminary Spearman correlation matrix. We selected the best-fitted GAMs considering only the variables that were significant and the highest possible R^2. The GAMs were performed considering first the whole study area and secondly the individual populations of Vilaflor and Arico, to detect possible local differences. For D_{1987} and D_{2016}, we performed a complementary Differential Local Moran's I in Geoda 1.8.16.4 to confirm the spatial correlation with D_{1963} and D_{1987} respectively.

2.3.2. Transects along elevational gradient

We compared the population structure of *Pinus canariensis* in the plots located at each zone, the montane forest, timberline, treeline and the isolated individuals using a non-parametric Kruskal-Wallis post-hoc Nemenyi test pair comparison. For that purpose, we used the PMCMRplus package in R Studio 1.0.136 (applying Bonferroni as *p*-value adjustment method and Chi-squared to correct ties) to obtain comparisons about pine height, DBH, D_{20} and mean crown diameter. We also tested differences in the ratio between D_{20}, DBH, and mean crown diameter with height, and performed Spearman correlations between all these measures with climatic and herbivory variables to detect possible local growing limitations.

3. Results

3.1. Remote sensing analysis

Overall we found a slow elevational advance and an increase in tree density in the whole study area from 1963 to 2016, with some spatial and temporal differences between localities (see Fig. 3). First, the treeline in Arico was considerably lower in elevation than in Vilaflor, starting around 2100–2200 m in 1963 and consolidating around the range of 2200–2300 m in the last picture. The number of plots with pines exceeding the 2300 m mark was only 4 in 1963, 8 in 1987 and 25 in 2016. In Vilaflor, upper limit of the treeline was around 2300–2400 m in 1963, with barely 4 plots with pines exceeding that belt. In 1987 and 2016 that number increased to 16 and 34 plots respectively. Horizontally, and considering the size of our grid (50 × 50 m), the expansion ranged between 50 and 550 m in the lower elevation transects (Arico), and between 50 and 250 m in Vilaflor. The number of pines in 1963 was especially low in Arico where isolated large individuals were found in many plots (mean value of 0.3 pines per plot versus 4 for Vilaflor). This difference in density of individuals among localities was maintained during all the spanned period, with 1.8 pines per plot in Arico versus 5.2 in Vilaflor in 1987 and 3.5 versus 7.3 pines per plot respectively in 2016. The shifts in pine density were constant in Arico during the periods of 1963–1987 and 1987–2016 with a variation of 1.6 and 1.7 in the mean number of pines per plot. However, in Vilaflor the mean increase almost doubled during the second period reaching a variation of 2.1 pines per plot from 1987 to 2016, while it was only of 1.2 during the first period (see Fig. 4).

The results of the GAM analyses combining all the considered variables were different across the study area, with values for the amount of deviance accounted ranging from 0.34 to 0.82 (see Table 1). The GAMs revealed clear positive relationships between pine density at each year (D_{1987} and D_{2016}) and the previous density of individuals (D_{1963} and D_{1987} respectively). The complementary Moran's I values calculated for these variables ranged between 0.333 and 0.338 (Vilaflor) and 0.432 and 0.605 (Arico), always with positive z-values. Thus, the pines were spatially grouped with respect to the population density of the previous years. GAMs also revealed in all the cases a positive relationship with temperature. Other variables such as precipitation, slope and geology were also significant but showed a more erratic behavior, having a negative or positive relationship depending on the locality. In regards to aspect, east and southeast were the most

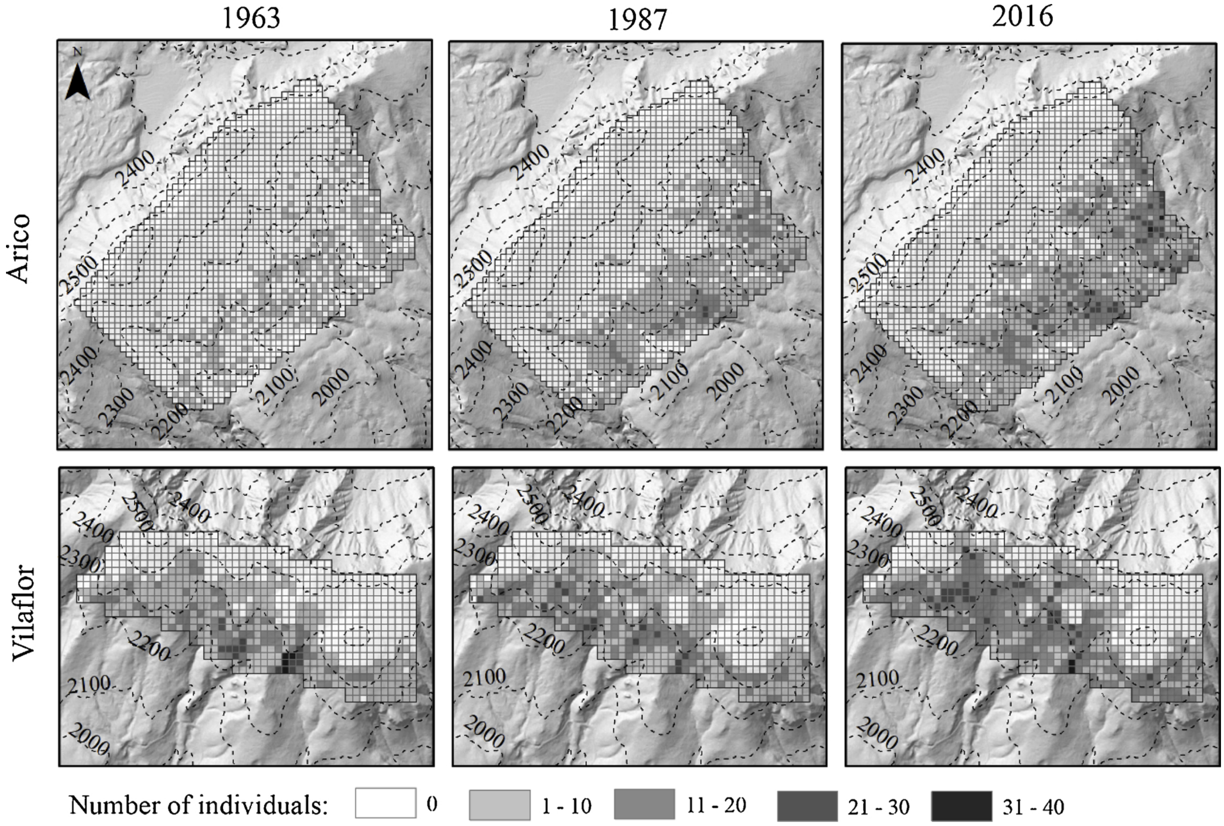

Fig. 3. Chronosequence of the treeline pine density in Arico and Vilaflor in the three aerial photographs selected.

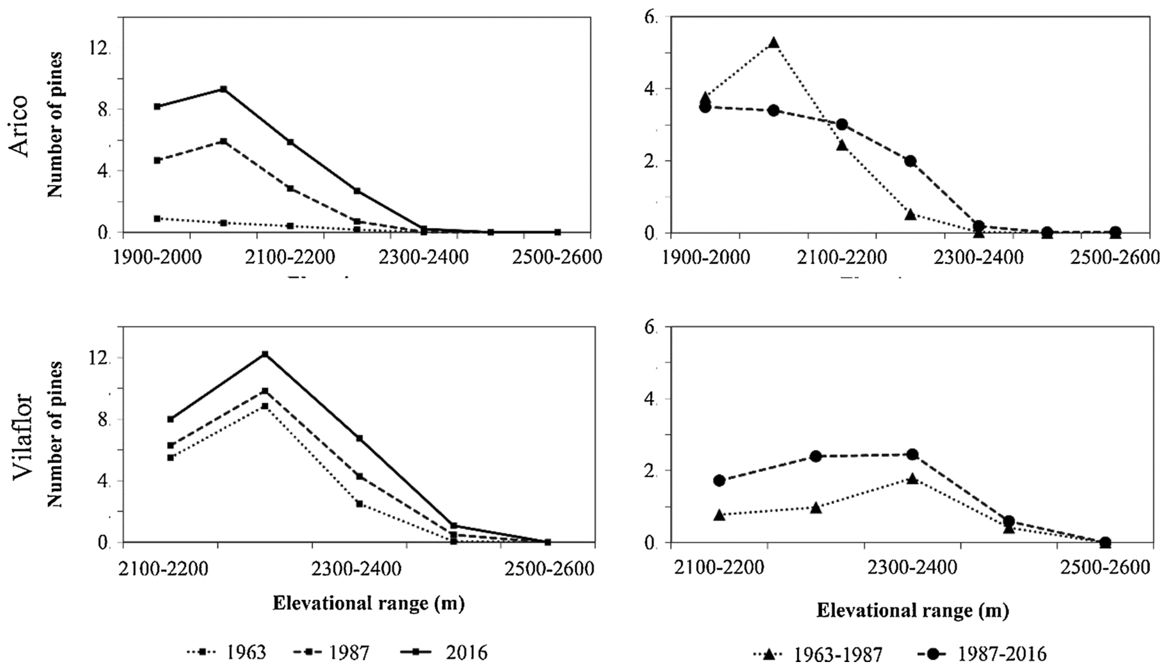

Fig. 4. Mean density of pines per year (D) and mean difference in the number of pines per period (ΔD) found by altitudinal ranges in the two study localities.

Table 1

Beta values of the significant variables ($p < 0.05$) used in the generalized additive models that are influencing the number of individuals in 1987 and 2016 for the whole study area and the two localities (Arico and Vilaflor) with their respective R^2 values. The shortened variable names that appear in the table correspond to the density of pine individuals in 1963 and 1987 (D_{1963} and D_{1987}); the mean annual, maximum and minimum temperature (T_{ann}, T_{max} and T_{min}); annual precipitation and that from the wettest and driest periods of the year (P_{ann}, P_{wet} and P_{dry}); the distance to areas affected by fire (*DTF*); and lithology classified by type of materials (L_{mat}; loose deposits or more solid materials) and by type of composition (L_{com}; siliceous or basaltic rocks).

	1987			2016		
	General	Arico	Vilaflor	General	Arico	Vilaflor
Intercept	−45.80	−3.56	6.78	−15.92	−26.69	−48.86
D_{1963}	0.67	1.00	0.60	–	–	–
D_{1987}	–	–	–	1.13	1.13	1.12
T_{ann}	3.64	–	–	1.72	0.23	–
T_{min}	–	0.29	0.37	–	–	–
T_{max}	–	–	–	–	–	0.18
P_{ann}	0.01	–	−0.02	−0.01	–	–
P_{wet}	–	–	–	–	–	–
P_{dry}	–	0.25	–	–	–	0.48
DTF	–	–	–	−0.24	–	–
Slope	–	−0.05	0.04	–	0.03	–
Aspect	1.21	0.53	−1.29	0.47	0.80	–
L_{mat}	–	–	–	–	−0.65	0.58
L_{com}	0.28	–	–	–	–	–
R^2	0.54	0.34	0.67	0.80	0.77	0.82

correlated orientations with density in most of the GAMs, excepting for the locality of Vilaflor in 1987, in which was north. *DTF* was negatively correlated with density in 2016 when both localities were considered together, meaning that it could exist certain positive influence of fire in pine density when distance is short to the affected areas.

3.2. Transects along elevational gradient

We found a negative gradient of seedlings density towards the summit areas and a lack of several height classes in the plots located at highest elevations (see Fig. 5). In them, they showed a maximum number of individuals from 2 to 20 m height, suggesting a slow colonization in the past and apparent difficulties for replacement and advance in elevation. In the montane forest and timberline plots, there is also a decrease in some classes, showing a two-mode structure with higher values for seedlings and individuals from 2 to 20 m height. Positive correlations ($r^2 > 0.7$; $p < 0.05$) were found between height and the other variables measured (D_{20}, DBH and mean crown diameter). According to Kruskal-Wallis post-hoc tests, the D_{20} and DBH in the montane forest plots were significantly lower ($p < 0.05$) than in the other plot types, since as is shown in the Fig. 5 there is a higher proportion of small and medium size individuals. The trend was not so clear for height, as two significant groups were observed, one for montane forest, treeline and isolated individuals plots, and another group for timberline and, again, isolated individual plots. The ratio relationships between pine height and D_{20}, DBH or crown presented a pattern of decreasing mean values with respect to elevation, which reveals a possible height growing limitation near to the summit. In this sense, trees from the treeline and those isolated, were significantly different in all those relationships ($p < 0.05$) from those of the montane forest and timberline, as they were slightly stumpier. Interestingly, seedlings (< 75 cm) showed a significantly lower ratio between height and side diameters than those of the following classes ($p < 0.05$), which could be revealing important growth problems at this stage. The minimum value in that relationship was found in the upper elevational plots, which could explain the increase of the low number of individuals in some classes at these elevations, as showed in the Fig. 5. Mean temperature was the only environmental variable that also explain growing limitation on the pines above 75 cm, as it was positively correlated with mean pine height ($r^2 = 0.262$) and mean ratio between height and D_{20} ($r^2 = 0.436$), DBH ($r^2 = 0.617$) and crown diameter ($r^2 = 0.410$). For seedlings lower than 75 cm, the mean ratio height-side diameter was positively correlated with maximum temperature ($r^2 = 0.378$) and negatively with the index of abundance of rabbits ($r^2 = -0.376$).

We also found a positive correlation between elevation and abundance of herbivores ($r^2 = 0.276$ for rabbits and $r^2 = 0.260$ for mouflons), that ranged from 0 to 4 in the scale of Cooke et al. (2008) for rabbits, and from 0 to 2 for mouflons. Differences in the herbivory

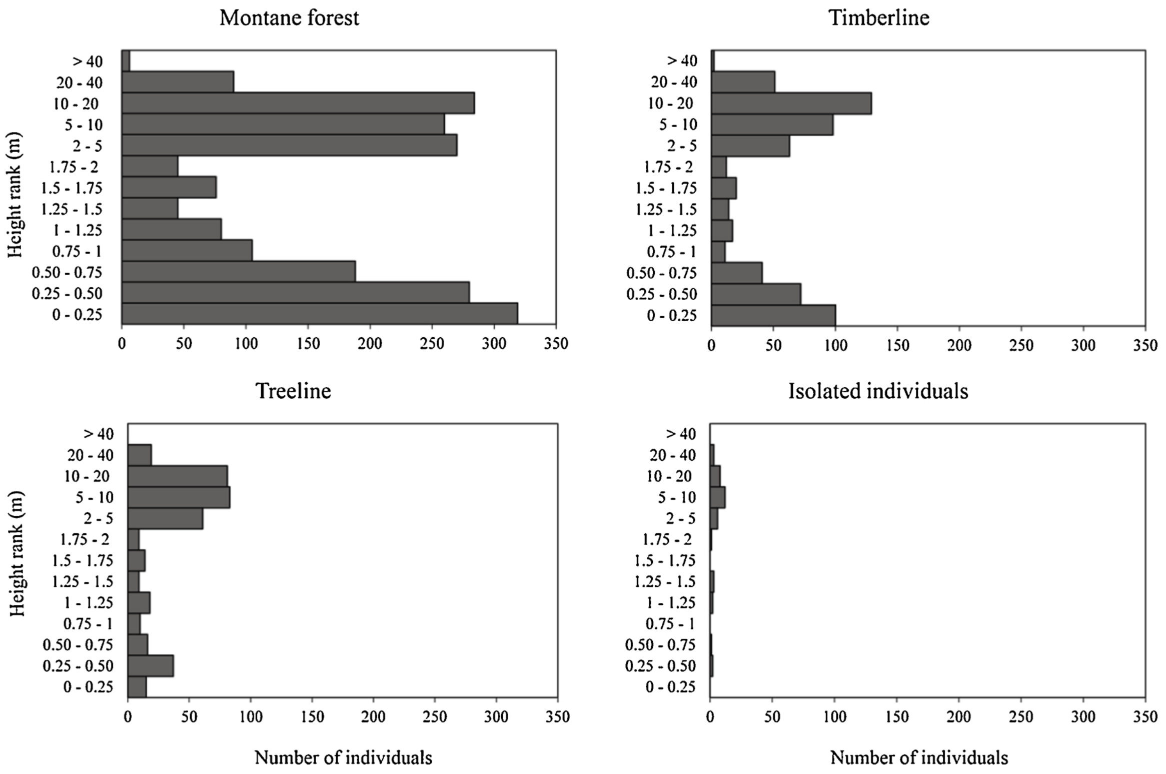

Fig. 5. Number of individuals classified by height in the four different forest categories.

abundance were not significant between montane forest and timberline; and between treeline and isolated individuals. On the contrary, significant differences ($p < 0.05$) were obtained when compared montane forest with treeline or isolated individuals plots. Negative Spearman correlations ranging r^2 values from 0.24 to 0.44 were found between number of juveniles of classes under 75 cm height and the abundance indices of both invasive herbivores. Interestingly, alpha diversity of the plots, which was always higher in the summit, was positively correlated to the index for rabbits ($r^2 = 0.294$; $p < 0.05$). Mean proportion of damaged individuals reached 26.4% in the montane forest plots (where there were more juveniles), 12.7% in the timberline plots, 9.7% in the treeline plots and 7.9% in the isolated individuals plots. These proportions drastically change if we consider only those pine individuals that may be browsed partially or totally by the herbivores (up to 2 m height), with values of 47.5%, 27.9%, 28.1% and 33.3% respectively. If we consider only those individuals under 75 cm (and therefore with true potential for being browsed by rabbits) mean percentages of damaged individuals increase to 68.5%, 37.9%, 52.9% and 100.0% respectively.

4. Discussion

Our study reveals the importance of considering historical remote sensing information for treeline shifts assessment. Despite previous studies highlighted the difficulties of the Tenerife's treeline to ascend in elevation in the northern slope of the island (Šrůtek et al., 2002; Gieger and Leuschner, 2004; Brito et al., 2014, 2016), our study concludes that at least during the last five decades there has been a general redensification of the natural treeline of the southern slope accompanied by a slow but consistent advance in elevation of isolated individuals. This process of redensification has occurred despite the existence of some limiting factors beyond the treeline such as lack of healthy rates of regeneration, absence of some tree height classes, limited growing or strong presence of herbivores.

The remote sensing analysis allowed us to identify the main factors driving those shifts in pine density. Among them, we found a strong spatial correlation between past and current pine populations on the study area. Despite we selected well-preserved stands of pine forest, it is very likely that the distribution of adults in the past was highly influenced by human activity as it happens in many treelines (Holtmeier and Broll, 2005; Gehrig-Fasel et al., 2007; Harsch et al., 2009). For instance, logging could be explaining the remarkable low number of trees in Arico area in 1963. The existence of enough nearby individuals is a key aspect in the regeneration dynamics of expanding forests that have been managed in the past (García et al., 2014; Bello-Rodríguez et al., 2016). That explains the faster spread of the forest found at lower elevation areas of the treeline in our study, where healthier and old individuals are available and besides the herbivores are less abundant and current environmental conditions more suitable.

Remote sensing analysis also revealed a positive influence of temperature, being this variable one of the key factors driving the spreading in elevation of treelines around the world (Danby and Hik, 2007; Harsch et al., 2009). Despite the current warmer and drier climate scenario in Tenerife (Martín et al., 2012; Santana and Martín, 2013), we can conclude that, in the spanned chronosequence, the forest spreading has not been limited in the treeline ecotone and it is occurring along the entire spanned elevational gradient. Previous works have considered the temperature as the main variable driving the expected rise in elevation of this forest from a climatophilous point of view (Del Arco and Garzón-Machado, 2012; Del Arco and Rodríguez, 2018). On the contrary, for precipitation we didn't find a clear trend restricting or ensuring the success of the species in the treeline ecotone. At local scale, it is very likely that extreme temperatures combined with drought will continue to be among the most important factors limiting regeneration at Tenerife treeline (Gieger and Leuschner, 2004; Köhler et al., 2006; Holtmeier, 2009; Brito et al., 2014; Wieser et al., 2016) and causing limited growing in adults (Hollermann, 1978; Šrůtek et al., 2002; Wieser et al., 2016). However, previous studies have demonstrated the high capacity of *P. canariensis* to adapt to very arid climates (Climent et al., 2002; López et al., 2008). In fact, global warming can also bring new opportunities for the expansion of the species such as lower frequency of frost (Martín et al., 2012), a greater cone opening due to heat waves (Barbour et al., 2012) and the possibility of colonizing the volcanic "caldera" of Mt. Teide, where the relief drastically descends to 2000 m. In this context, recruitment in these areas could be increasingly dependent on the rainy years and the possible nurse effect of the same or other shrubby species as it happens in many other arid and alpine environments (Callaway et al., 2002; Castro et al., 2004; Flores and Jurado, 2009).

Additionally, we also found a weak but positive influence of one fire that affected partially our study area. Fires have become very frequent during the last decades in the Canary Islands (Quirantes et al., 2011; ISTAC, 2018) and it has been demonstrated that fire can locally and temporary enhance the regeneration of *Pinus canariensis* and change the understory species composition (Hollermann, 2000). Although regeneration of this species is not necessarily dependent on the existence of fire (Méndez, 2010) and Barbour et al. (2012) demonstrated that is not a pyrophyte, fire could partially benefit *P. canariensis* and other understory species thanks to a temporary reduction of herbivore effects.

Population structure analyses also revealed interesting findings about the herbivores effect. As it has been found in other areas, herbivore browsing represents an additional factor limiting regeneration in the treelines (Grace et al., 2002; Cairns et al., 2007; Gehrig-Fasel et al., 2007; Speed et al., 2010). We found a clear increase in invasive herbivores abundance (*Oryctolagus cuniculus* and *Ovis orientalis*) from the montane forest area to the summit, with higher proportions of damage in pines (< 75 cm) in the summit areas. So, invasive herbivores, especially rabbits, can be pointed out as another reason limiting growth and regeneration on the treeline ecotone. Rabbits and mouflons are already one of the most important conservation problems in El Teide National Park as they are rapidly modifying the natural plant species composition (Rodríguez-Luengo, 1993; Cubas et al., 2017). At the same time, they are also well known for their role on the current impoverishment of the understory of the Canarian pine forests (Garzón-Machado et al., 2010). In our case, rabbits were more abundant and widespread than mouflons, and the trends point out that their populations will be enhanced at higher elevations due to global warming (Bello-Rodríguez et al., 2019).

5. Conclusions

Thanks to the use of historical aerial photography, our study concludes that *P. canariensis* is slowly but successfully advancing in elevation since the 60s and interestingly, a process of redensification is occurring under the current treeline. Considering several factors that are influencing the species at this elevation, we can conclude that its establishment beyond the last line of the forest is depending on: (1) the density of individuals and forest structure derived of the past, which can enhance seed and safe sites availability, (2) the browsing produced by rabbits and mouflons, (3) the decline in the frequency of extremely low temperatures, and (4) the maintenance of a low human pressure. In conclusion direct and indirect human impacts are responsible for the density and distribution of the endemic pine forests of the Canary Islands.

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