



RESEARCH ARTICLE

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Species turnover during secondary succession in a laurel forest stand 50 years after clearcutting

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Abstract

Aim of study: The present study was designed to evaluate the effects of clearcutting and recovery of a laurel forest stand, 50 years after felling.

Area of study: Laurel forest stand in Agua García, Tenerife (Canary Islands)

Material and methods: Structural stand parameters were measured in a large patch of laurel forest.

Main results: The results revealed that *Erica arborea* and *Ilex canariensis* have acted as pioneer species in the broad sense of the term, while *Morella faya* has remained abundant throughout the study. *Persea indica* became increasingly dominant throughout succession, as indicated by several different structural parameters.

Research highlights: Recovery of the laurel forest after clearcutting has been possible in some areas without any further forest management, as indicated by the species composition and forest structure.

Key words: Canary Islands; Ecological Restoration; Laurel forest; Succession.

Citation: Arévalo, .J.R.; Aboal, J.R. (2015). Species turnover during secondary succession in a laurel forest stand 50 years after clearcutting. Forest Systems, Volume 24, Issue 1, e-007, 5 pages. http://dx.doi.org/10.5424/fs/2015241-05776.

Received: 18 Feb 2014. **Accepted:** 15 Dic 2014 http://dx.doi.org/10.5424/fs/2015241-05776

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Funding: The authors received no specific funding for this work.

Competing interests: The authors have declared that no competing interests exist. Correspondence should be addressed to Jose Ramon Arévalo: jarevalo@ull.edu.es

Introduction

Clearcutting is defined as anthropogenic disturbance that converts a forest stand to an early successional stage and is known to have potentially important environmental impacts (Smith *et al.*, 1997). Most experimental or comparative studies of the effects of such disturbance have shown that the highest levels of species diversity were maintained at an "intermediate" frequency of intensity of disturbance (Huston, 1994).

The structure and dynamics of laurel forest in the Canary Islands have not been widely studied, and research carried out to date has focused on spatial patterns, seed banks, regeneration and gap dynamics (Ohsawa *et al.*, 1999; Arévalo & Fernández-Palacios, 1998). Today, only 10% of the original laurel forest on the island of Tenerife remains unaltered (Santos, 1990). Study of a laurel forest unmanaged since clearcutting

provides a valuable opportunity to learn more about the long-term dynamics of laurel forest, as succession following this type of disturbance may be similar to succession following other types of stand replacement or gap openings.

Because of the lack of information about the impacts of clearcutting in laurel forest, we used a long-term data set to test the following hypotheses: i) *Erica arborea* and *Morella faya* act as pioneer species and their dominance in terms of both density and biomass decrease throughout succession, and ii) 50 years after clearcutting, the stand has recovered the status of laurel forest as indicated by the species composition and richness. Because the present study was designed to evaluate the effects of clearcutting in a laurel forest, we restricted the study to the only available plot with this site history and with characteristics representative of laurel forest.

Material and methods

Study site

The irregularly shaped experimental plot covers an area of 3390 m² within a rectangle of 110 x 50 m (centre of the plot, UTM x=362464; y=3148692 WGS84). The plot is described in more detail elsewhere (Morales *et al.*, 1996). The vegetation is representative of valley-bottom laurel forest. The nomenclature follows that proposed by Arechavaleta *et al.* (2010).

The climate is humid Mediterranean with an annual mean temperature of 14.0°C, an annual mean relative humidity of 80%, and a mean annual precipitation of 733 mm. The soil in the plot originates from bedrock that is a mixture of olivine basalt and pyroclast and is classified as an allophanic andosol.

Although data on the original stand before clearcutting was not available, the study site was presumably occupied by typical valley bottom laurel forest with *Persea indica, Laurus novocanariensis, Morella faya...* (Arévalo & Fernández-Palacios, 1998), but some information can be found in Brito and Vicente-Lope (1995). The plot was clearcut in 1963, and is now surrounded by a matrix of laurel forest and is also close to plantations of *Pinus radiata* and *Eucalyptus cameldulensis* and *E. globulus*.

Data collection

After identification of the species present, diameter at breast height (DBH) was measured in June of 1993, 1995, 1997 and 2013. During the first inventory, the height at which DBH was determined was marked with indelible paint on each stem. All measurements were then made at the same height in all subsequent inventories. All stems were also numbered and marked. Heights of trees and heights of the crown of the trees were also measured in 1993, 1997 and 2013 with the aid of a Blume Leiss hypsometer. The above ground biomass (AGB) was estimated using allometric equations developed by Aboal et al. (2005) for E. arborea, I. canariensis, L. novocanariensis, M. faya and P. indica. As no equation has been developed for I. perado ssp. plathyphylla, the equation developed for I. canariensis was used to estimate the AGB of this species.

Data analyses

We applied the Shannon-Wiener diversity index, which is based on density calculations and also on the AGB of the trees. Survival rates indicate the proportion of trees surviving from the start of each period studied.

For indirect gradient analysis, we used Detrended Correspondence Analysis (DCA) in CANOCO (ter Braak & Šmilauer, 1998) to examine how species composition changes throughout the 50-year sampling period. We based the analysis on the importance index (the sum of the percentages of basal area, density and AGB divided by three).

Results and discussion

Six tree species have been identified in the plot in the past 20 years. The AGB increased twofold, while the BA increased by 61% (Table 1). After 1993 (40 years after clearcutting), the dominant species, in terms of tree density, was L. novocanariensis, followed by E. arborea. In the same period, the dominant species based on AGB was M. faya, followed by L. novocanariensis, and the same pattern was observed for basal area (Table 1). At present (i.e. 50 years after clearcutting) the dominant species are P. indica in terms of DBH, M. faya in terms of AGB, and L. novocanariensis in terms of density. During the last 20 years, 56% of the trees have died and there has been no new recruitment (DBH>4cm) of the tree species growing in the plot. The Shannon index (expressed as e^{H'}) has decreased greatly over the years, especially in the last sampling period, when calculated on the basis of both density (8.13, 8.15, 8.14, 5.98 for 1993, 1995, 1997 and 2013 respectively) and biomass (6.81, 6.86, 6.60, 5.36 for 1993, 1995, 1997 and 2013 respectively). This decrease in biological diversity was mainly caused by the disappearance of some species (i.e., I. canariensis and E. arborea) and the increasing dominance of other species (i.e., P. indica and M. faya). Morella faya has remained the most abundant species throughout all the sampling periods (based on basal area, AGB and density; Table 1) and is one of the tallest trees. Thus, in a period of only 20 years the pioneer species have largely been replaced by late successional species, thus indicating that the stand has continued to change in species composition.

Throughout the last 20 years, the DBH of the late successional species (*L. novocanariensis*, *P. indica*) and some intermediate successional specis (*M. faya* and *I. perado*) has increased, although the dominant species has always been *M. faya*, followed by *P. indica*. The same species always yielded the tallest trees over the years. Crown height has been found to be more variable, and although the dominant species based on top height were initially *I. canariensis* and *I. perado*, these have been replaced by *L. novocanariensis* and *P. in-*

Table 1. Absolute values and percentages (in brackets) of stem density (stems ha⁻¹), above ground biomass (AGB) (Mg ha⁻¹) and basal area (BA) (m² ha⁻¹) for each of the species growing in the experimental plot. The plot total for each of the sampled years and median and median absolute deviation (in brackets) of the DBH (cm), top height (TTH) (m) and crown height (CH) (m) are also shown for each of the species growing in the experimental plot (Ea: *Erica arborea*; Ip: *Ilex canariensis*; Ip: *Ilex perado* ssp. *platyphylla*; Ln: *Laurus novocanariensis*; Mf: *Morella faya*; Pi: *Persea indica*).

	Year	Ea	Ic	Ip	Ln	Mf	Pi	Plot total
Density	1993	469 (28%)	27 (2%)	41 (2%)	640 (38%)	283 (17%)	239 (14%)	1699
	1995	469 (28%)	27 (2%)	41 (2%)	628 (37%)	280 (17%)	233 (14%)	1678
	1997	336 (23%)	21 (1%)	35 (2%)	584 (39%)	280 (19%)	224 (15%)	1481
	2013	18 (2%)		18 (2%)	322 (43%)	215 (29%)	180 (24%)	752
AGB	1993	25.4 (16%)	2.0 (1%)	2.3 (1%)	47 (26%)	74.6 (47%)	14.2 (9%)	159.2
	1995	27.1 (15%)	2.2 (1%)	2.6 (1%)	49.8 (27%)	83.2 (46%)	17.5 (9%)	182.5
	1997	22.7 (12%)	2.2 (1%)	2.6 (1%)	57.0 (29%)	91.0 (46%)	19.9 (10%)	194.5
	2013	3.6 (1%)	0.0 (0%)	2.8 (1%)	106.8 (34%)	139.0 (41%)	74.5 (23%)	318.6
BA	1993	6.56 (20%)	0.34 (1%)	0.38 (1%)	8.44 (25%)	12.84 (39%)	4.65 (14%)	33.21
	1995	7.00 (19%)	0.37 (1%)	0.42 (1%)	9.82 (26%)	14.18 (38%)	5.48 (15%)	37.27
	1997	5.88 (15%)	0.36 (1%)	0.42 (1%)	10.8 (28%)	15.22 (39%)	6.03 (16%)	38.7
	2013	0.95 (2%)		0.44 (1%)	15.65 (29%)	20.73 (38%)	16.97 (31%)	54.74
DBH	1993	13 (2.8)	9.8 (1.1)	8.6 (1.4)	12 (3.0)	23.4 (4.2)	14.5 (3.3)	13.5 (10.5)
	1995	13.5 (3.0)	10.3 (1.3)	8.8 (1.5)	12.5 (3.5)	24.5 (4.1)	16.0 (4.0)	14.6 (11.4)
	1997	14.7 (2.5)	10.8 (0.4)	9.5 (2.4)	13.8 (3.8)	25.3 (4.4)	17.2 (4.3)	16.0 (12.4)
	2013	23.5 (3)		15.5 (6.8)	22.3 (5.5)	34.4 (5.6)	33.3 (7.7)	29.0 (23.0)
TTH	1993	12(1)	12.5 (1.5)	11.8 (1.8)	13.5 (1.5)	14.5 (1)	14 (1.5)	13 (1.5)
	1997	13.5 (1.5)	14(0)	12.8 (4)	16 (1.5)	16.5 (1.5)	16 (1.5)	15.5 (1.5)
	2013	19.8 (2)	_	16.3 (4.3)	23.5 (3)	24.5 (3.5)	29.5 (2)	24.5 (4)
СН	1993	3.0 (1.0)	3.0 (3.0)	2.8 (0.8)	4.0 (1.0)	4.0 (1.0)	4.0 (1.0)	3.5 (1.0)
	1997	2.5 (1.0)	2.3 (2.3)	3.3 (1.0)	4.0 (1)	4.5 (1.5)	4.8 (0.8)	4.0 (1.0)
	2013	0.5 (0.0)	_	8.8 (4.0)	4.0 (1.5)	3.5 (1.0)	7.0 (2.0)	4.5 (1.5)

dica (Table 1). Therefore, *M. faya* should be considered a relatively long-lived pioneer species, because it was present during the early stages of the sampling, but still remains in this later successional stage after 50 years, and was not replaced during the intermediate phases of the succession. Also, we did not find regeneration for these species in the last sampled periods.

The probability of survival of the trees during the period considered also varied among species: I. canariensis 0%; E. arborea 4%; I. perado 43%; L. novocanariensis 50%; P. indica 75% and M. faya 76%., The number of trees dying during the period 1993-95 was very low (Figure 1, probability of survival ranged between 98 and 100%), while during the period 1995-97 the mortality increased, especially in individuals of E. arborea (probability of survival, 72%, which corresponds to a mortality rate of 142 ‰) and those of the genus Ilex (probability of survival ca. 85%). The survival rates of other species were higher than 90% (Figure 1). Furthermore, the probability of survival is not the same for all individuals of the same species. but rather increases with the initial size of the tree (Figure 1). In addition to the structural characteristics of the species, we have revealed changes in species composition throughout the sampling period.

The change in species composition followed similar patterns based on the importance value (Figure 2). We identified E. arborea and I. canariensis as dominant species after 40 years of natural stand dynamics (displaced in the bidimensional space of the DCA as an important species for 1993) and P. indica and L. novocanariensis as dominant at a later successional stage (50 years). The other species were more or less intermediate in terms of successional changes. Species turnover appears to have been governed by competition. The ability of some species to alter the allometric relationship between DBH and tree height enables them to obtain light in the upper layers of the canopy. On the other hand, some species (i.e. E.arborea and *I.canariensis*) reached the canopy level and then died and were replaced by characteristic late successional species such as *P. indica* and *L. novocanariensis*.

Our results reveal that an intermediate successional status of mature laurel forest has been reached (compared with natural laurel forest; Arévalo & Fernández-Palacios, 1998) as a result of some favorable conditions: the low intensity of disturbance (spatial and temporal); a well-conserved (although not adjacent) surrounding matrix of laurel forest (beyond the limits of the exotic plantions) that characteristically (Car-

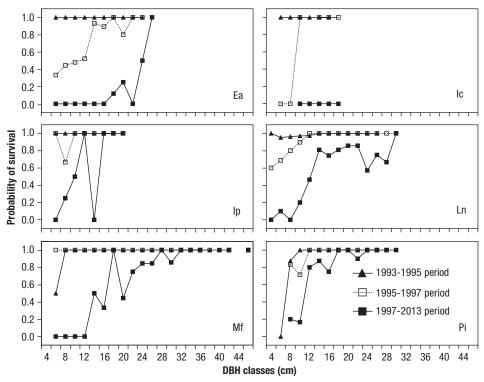


Figure 1. Mean survival probability for each DBH class (cm; the central size in each class is shown) of six major species (species indicated in Table 1). The DBH at the start of each period is shown (black triangles and solid line: 1993-1995; empty squares and dotted line: 1995-1997; black squares and dotted line: 1997-2013).

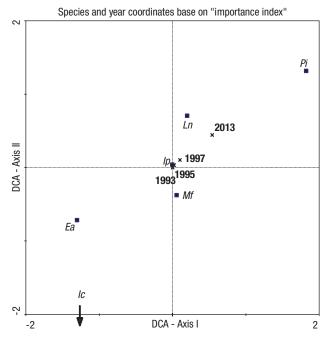


Figure 2. DCA of species and sampling period scores for importance value (eigenvalues of axes I and II: 0.06 and 0.01 respectively, and the percentage of total inertia explained, 99.5%). Species indicated in Table 1.

valho, 2002) provides a constant source of propagules from bird dispersion (Arévalo & Fernandez-Palacios, 2005); and maintenance of species richness due to

vegetative regrowth, which is also characteristic of the tree species that comprise laurel forest.

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