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## Original article

# Laurel forest recovery during 20 years in an abandoned firebreak in Tenerife, Canary Islands

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## ABSTRACT

This study assessed the recovery of the structure and species composition of a laurel forest in an abandoned firebreak in the Rural Park of Anaga, Tenerife (Canary Islands). We statistically compared values of species richness, density and biovolume between 23 plots in the firebreak and six control plots in natural forest near the firebreak. We evaluated changes in species composition with detrended correspondence analysis (DCA) based on densities and biovolume. Biovolume is increasing significantly along the successional gradient (from 1990 to 2004) but remains less than the values in control plots. Stem densities were significantly lower in control plots than in 2004 plots. Species richness was significantly higher in control plots than in 2004 plots (although there were no differences in values obtained between the first sampling period 6 years after abandonment, and the second sampling 20 years after abandonment). Changes in species richness are significant, but all species present in control plots are also found in the firebreak plots. DCA based on biovolume significantly discriminated control plots from firebreak plots in 1990 (for axis 1). Results suggest recovery to a laurel forest is occurring, although more time will be required to reach control plot density and biovolume values. The low intensity of disturbance and a well-conserved forest adjacent to the firebreak favour the recovery of species inside the firebreak. We advise eliminating suckers from all small trees (leaving the bigger stems) to accelerate succession to a vegetation structure similar to that found surrounding the firebreak.

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## 1. Introduction

Today, habitat loss, primarily due to deforestation and land use changes, is considered one of the most important threats to species diversity in the world (Gurevitch and Padilla, 2004).

The construction of roads and trails can result in habitat loss. Roads and trails can also act as corridors or habitat for species not found in the undisturbed forest matrix (Forman et al., 2002; Forman and Alexander, 1998; Spellerberg, 1998). Despite some ecological similarities, forest firebreaks are clearly

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different from other anthropogenic corridors (e.g. less impact on soil, constant dispersion of propagules onto the firebreak). Whereas the restoration of roads requires active and intense intervention (Holl et al., 2000; Switalski et al., 2004) due to the impacts of traffic on soil characteristics, dispersion of exotic species, elimination of a native seed bank, elimination of area due to pavement and other factors (Milberg and Lamont, 1995), the impacts of firebreaks on the forest are, in contrast, lower and restoration can be accomplished with minimal to no management following abandonment.

Today only 10% of the original laurel forest on Tenerife Island remains unaltered (Santos, 1990). While natural disturbances and regeneration in laurel forests have been studied (Arévalo and Fernández-Palacios, 1998; Arévalo et al., 1999; Arévalo and Fernández-Palacios, 2003), many of the long term dynamics of laurel forests, like other mountain cloud forests elsewhere, are largely undescribed (Hamilton et al., 1995). Regeneration after disturbance is one of the principal factors that structures plant communities (Terradas, 2001). The study of an abandoned firebreak offers a valuable opportunity to learn more about the long-term dynamics of a laurel forest since succession following this disturbance could be similar to succession following other disturbances such as gap openings in the canopy.

The main aim of this study is to describe the recovery of the structure of the vegetation (density and biovolume) and species composition after a 20-year period following the disturbance (no machinery, but manual clearing of the firebreak at intervals of 3–5 years). Also, the firebreak is surrounded by a well conserved forest matrix and asexual regeneration through basal resprouting, which is common in this type of vegetation, can help this recovery. Application of our study results could help guide the development of restoration plans, land reclamation planning and the formulation of recommendations for plantations.

## 2. Materials and methods

### 2.1. Study site

The study was conducted in the Anaga Rural Park in the NE corner of Tenerife (Fig. 1), Canary Islands (28° 19' N, 16° 34' W). The park encompasses a 7–8 million year old basaltic massif (Ancochea et al., 1990) covering about 130 km<sup>2</sup>. The park represents 7% of Tenerife's total area. Tenerife's evergreen laurel forest has been extensively exploited since the arrival of the Europeans in the 15th century (Parsons, 1981). The 10% of the forest that remains has been formally protected since 1988 and is currently experiencing reduced human disturbance and no reduction in area. No data are available about the precise forest age, but aerial photographs from 1952 show the forest in its current state, in terms of both extent and physiognomy. In the 1940s, there was still some illegal, small-scale forest exploitation. Due to its present protection status and public use, the illegal forest exploitation that did occur was of limited extent (small scale).

The laurel forest is distributed between 600 and 900 m altitude and, depending on the slope, the canopy is 10–20 m in

height. Maximum canopy heights are found at valley bottoms, decreasing progressively towards the upper valley margins. The laurel forest of Anaga contains a total of 19 tree species (Santos, 1990). Dominant species include *Laurus novocanariensis*, *Erica scoparia*, *Erica arborea*, *Ilex canariensis*, *Prunus lusitanica*, *Myrica faya* and *Viburnum tinus*. The dominance of a given species depends on site conditions. For example, *E. scoparia* dominates on forest ridges, *L. novocanariensis* in mesic zones and *E. arborea* in more disturbed areas (Anon, 1973). Because the area of the firebreak is mainly in the southern aspect of the park, dominant species are *E. arborea*, *M. faya* and *I. canariensis*. Further information on stand composition, structure and environment in the study sites can be found in Arévalo (1998) and Arévalo et al. (1999). Species nomenclature follows Izquierdo et al. (2001).

The firebreak is located in El Moquinal. Its highest point is at 847 m asl. It runs 450 m north to south and is 10 m wide (Table 1). This firebreak was established in the 1960s when fire control was very popular and was maintained until its abandonment in 1984 (due to the low number of wildfires in the area). The original vegetation was a well conserved laurel forest similar to the one surrounding the present firebreak, and vegetation was cut to ground level. Maintenance was performed every 3–5 years by a team of 4–10 men. They cut all the vegetation in a 10 m wide band just above ground level.

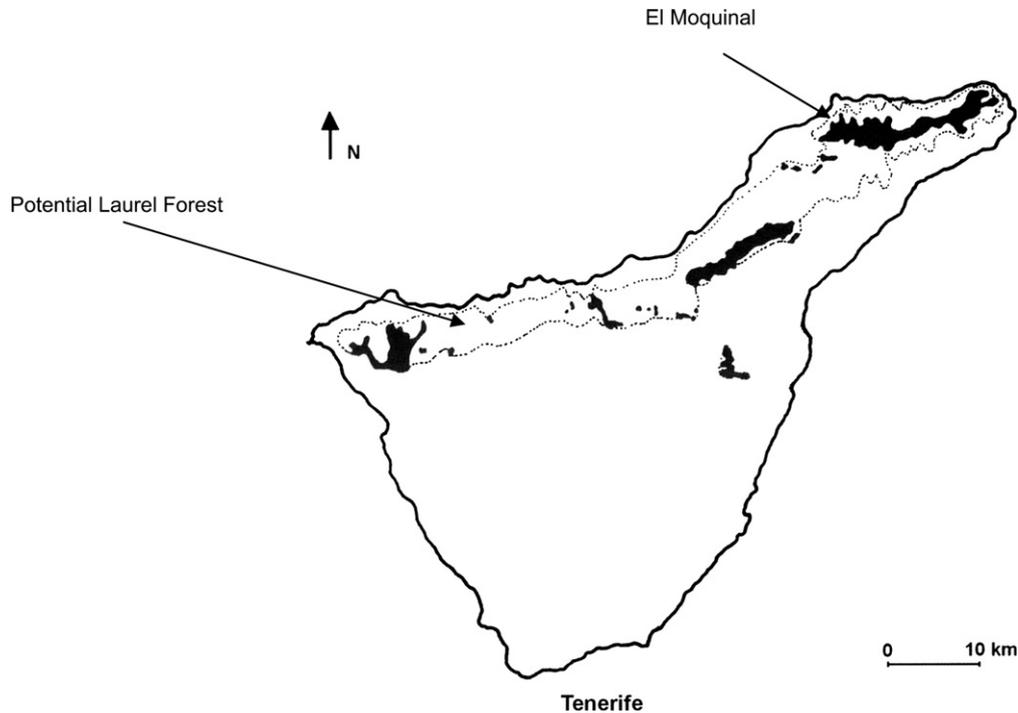
### 2.2. Sampling design

We established 23 2 × 8 m (16 m<sup>2</sup>) permanent plots in 1990 along the centre of the firebreak every 20 m from the highest point, starting from the border (the last one was located at 440 m). The long axis of each plot was parallel to the firebreak. The plots were numbered from 1 (at the highest point) to 23. In 2004 six control plots with similar dimensions were established at 50 m intervals at a distance of 10–15 m from the firebreak.

In each plot we counted and measured the height of all individuals present by species. We also measured the stem diameter along the larger axis and the perpendicular axis, in order to estimate the biovolume (Fernández-Palacios and de los Santos, 1996) of each individual plant in the plot. For shrubs and forbs, we measured the diameters from the top. For trees, we estimated the two axes from the projected canopy on the ground. The sampling was conducted from January to March in 1990 and in 2004, respectively 6 and 20 years after abandonment.

### 2.3. Soil parameters

Nutrient variability could explain the existence of different patterns of regeneration between different areas. We examined soil characteristics and nutrient availability across the plots to reveal possible effects on species distributions. We collected 1 kg soil samples in March 2004 from four randomly selected locations on the border of each plot by excavating to a depth of 15 cm. The four samples were combined to form a composite sample for the analyses. We sieved (>2 mm) the air-dried soil and aerobically stored each sample at room temperature. Litter covering the plot (not decomposed) was collected and weighed *in situ* and re-distributed over the plot



**Fig. 1 – Actual (bold) and potential (plain) distribution of the laurel forest on Tenerife. ‘El Moquinal’ laurel forest (firebreak location) station is located in the Anaga massif.**

(a small sample outside the plot was removed for humidity calculations).

We measured soil pH by glass electrode. Nitrates and ammonium were measured in an extraction of KCl (2 M) using the colorimetric method of Sims et al. (1995). Phosphorus was measured in extractions with  $\text{NaHCO}_3$  (0.5 M) at pH 8.5 following the Olsen et al. (1954) method.

#### 2.4. Statistical analysis

Ordination techniques help to explain community variation (Gauch, 1982) and they can be used to evaluate trends through time as well as space (Franklin et al., 1993; ter Braak and Šmilauer, 1998; Arévalo et al., 1999). We used detrended correspondence analysis (DCA; Hill and Gauch, 1980) of CANOCO (ter Braak and Šmilauer, 1998) to examine how species composition changed through space and time and whether different classes of samples could be extrapolated from the analyses. Analyses were based on species densities and biovolume.

Differences in nutrient content between control plots and firebreak plots were analyzed using the independent Student's *t*-test ( $P < 0.05$ ). Differences in density, biovolume and species richness between plots of different periods were analyzed using standard analysis of variance (ANOVA,  $P < 0.05$ ). Normality of the data was checked with the Shapiro-Wilk test, and homoscedasticity of the data was examined with an *F* test.

We analyzed if axes I and II significantly discriminated the groups using the coordinates of the plots at different periods and analyzing these coordinates with a logistic regression,

the response variable being the sampling period (1990 plots, 2004 plots or control-2004 plots). We tested for both axes the 1990–2004 plots, control–1990 plots and control–2004 plots.

Basic statistical methods followed Zar (1984) and were applied with the SPSS statistical package (SPSS, 1986).

### 3. Results

The area where the firebreak is located presents some variability in altitude (64 m). We can consider it a laurel forest community with the same species composition as other well conserved areas of the laurel forest (Table 1).

Changes after disturbance of the vegetation can be revealed through changes in structural parameters such as stem density, biovolume and species richness (Pickett and White, 1985). After 6 years of abandonment values for stem density in the firebreak did not differ from current values for the control plots (Fig. 2a), but they became significantly higher 14 years later ( $F_{2,49} = 26.704$ ,  $P < 0.001$ ). Density included woody plants (trees and shrubs) and forbs (no graminoids were found in the plots). Changes were graphically better reflected in the biovolume data (Fig. 2b), where significant changes were found from the first sampling to 2004 ( $F_{2,49} = 33.704$ ,  $P < 0.001$ ). Changes in species richness were significant ( $F_{2,49} = 6.399$ ,  $P < 0.003$ ; Fig. 2c). The post-hoc test indicated that species richness in the firebreak in 1990 did not differ from the species richness in the plots in 2004, but the control plot values were significantly higher than the firebreak values in 2004.

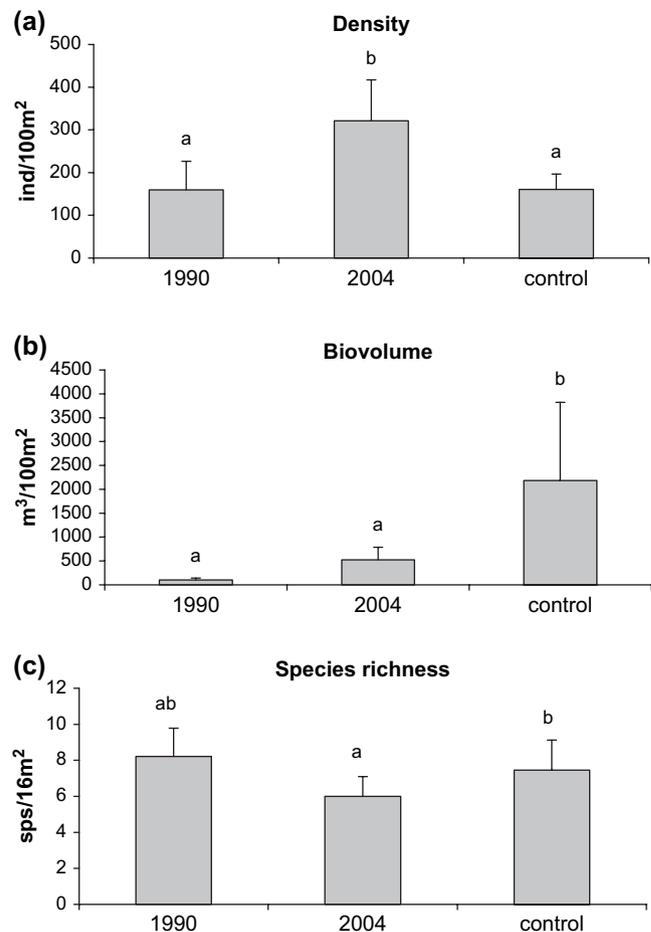
**Table 1 – General features of the plots**

Plot	Aspect	Location	Altitude
1	NW	Peak	845
2	NW	Peak	843
3	W	Side	836
4	NW	Side	826
5	S-SE	Side	817
6	N-NW	Side	809
7	SE	Side	805
8	S-SE	Bottom	800
9	S-SE	Bottom	799
10	N-NW	Side	798
11	S-SE	Peak	801
12	N-NW	Peak	802
13	N-NW	Peak	799
14	S-SE	Peak	796
15	S-SE	Peak	788
16	N-NW	Bottom	783
17	E	Bottom	781
18	N-NW	Bottom	782
19	N-NW	Bottom	786
20	E	Side	794
21	E	Peak	799
22	SE	Peak	798
23	E	Peak	799

Based on our own observations and the study results, much of the regeneration occurred by re-seeding (personal observation). Resprouting was less common although very important in some tree species such as *Erica arborea*. Due to the character of basal sprouting of the laurel forest species, it is possible to differentiate between asexually and sexually produced plants (Arévalo and Fernández-Palacios, 1998).

With respect to species composition based on density, the DCA bi-dimensional space defined by axes I and II indicated that disturbance due to the firebreak has increased species variability among plots (Fig. 3). Species such as *Lavandula stoechas*, *Convolvulus canariensis*, *Pteridium aquilinum* and *Rumex inermis* are characteristic of the plots at the beginning of the successional period. *Smilax* sp., *Hypericum grandifolium* and *Sonchus oleraceus* are characteristic of 2004 plots. Control plots cannot be discriminated from plots in the firebreak at either sampling period, indicating that almost all the species of the firebreak plots are present in the control plots, an indication of the dominance of woody species such as *Laurus novocanariensis*, *Myrica faya*, *Erica scoparia*, *Erica arborea* and *Ilex canariensis* (Fig. 3, Appendix A).

Analysis of species composition based on biovolume gave similar results to those for density. However, discrimination between groups of plots was clearer, indicating a stronger gradient and a higher proportion of the total inertia explained by axes I and II in the analysis (43.7% in this analysis vs. 35.3% in the analysis based in density). Three species were not included in this analysis due to their low values (*Sonchus oleraceus*, *Rubus inermis* and *Convolvulus canariensis*). In this case, discrimination among firebreak plots and control plots was more evident, and again, a higher variability in species composition was revealed in the firebreak plots (Fig. 4, Appendix A). The results of the logistic regression revealed

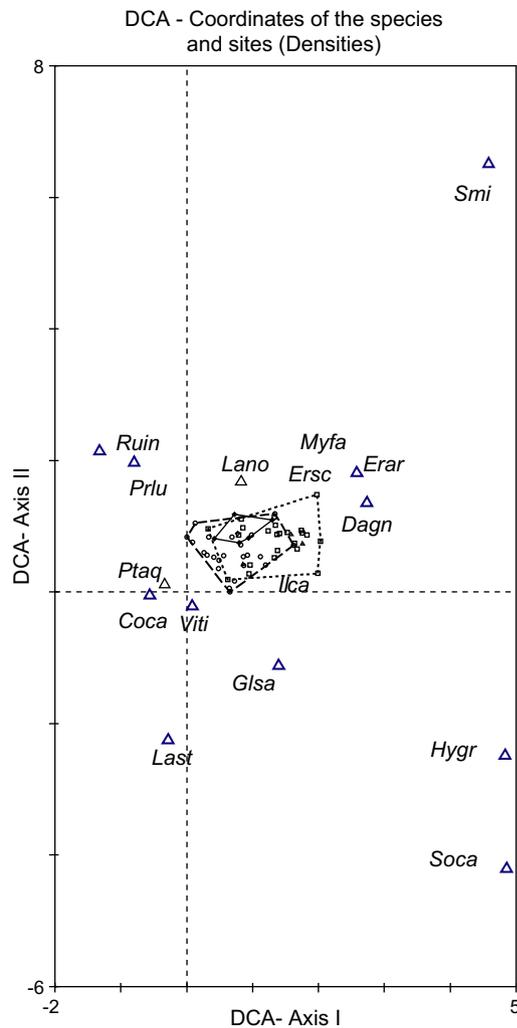


**Fig. 2 – Mean values and standard deviations for (a) density of plants (individuals/100 m<sup>2</sup>); (b) biovolume (m<sup>3</sup>/100 m<sup>2</sup>); and (c) species richness. Identical letters above the bars indicate non-significant differences.**

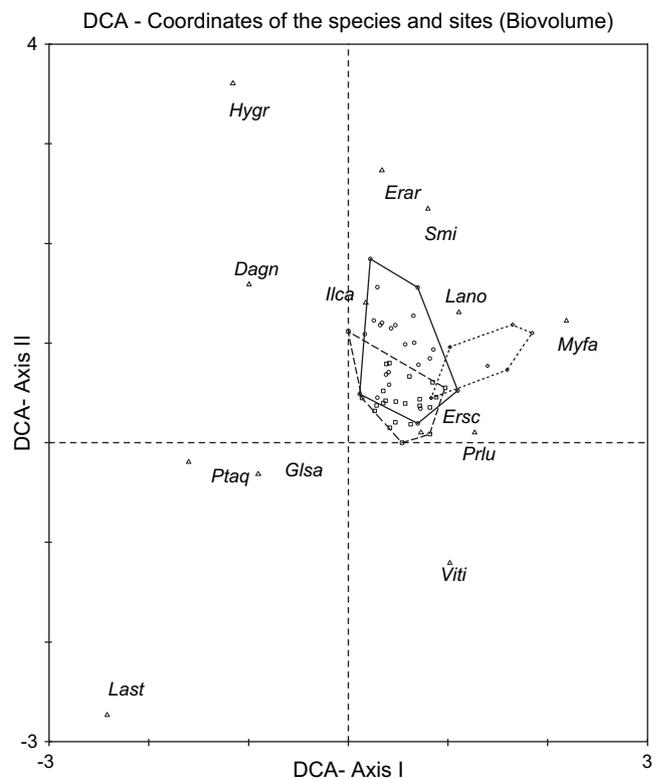
that control plots are discriminated from firebreak plots along axis I, while firebreak plots 1990 and 2004 are significantly discriminated along axis II (Table 3).

Tree species are characteristic of the control plots (*Laurus novocanariensis*, *Ilex canariensis*, *Myrica faya* and *Prunus lusitanica*), while the firebreak plots are characterized by forbs such as *Lavandula stoechas*, *Hypericum grandifolium*, *Globularia salicina* and *Daphne gnidium*. However, all the species are present in both sets of plots.

Analysis of basic nutrients in the soil for firebreak and forest plots in 2004 indicated that firebreak soils will require more time to attain nutrient conditions similar to unaltered areas. Nitrates, ammonium and phosphorus levels were significantly lower in firebreak plots than in control plots ( $P < 0.01$ ), while pH did not differ significantly between firebreak and control plots ( $P > 0.05$ ). These changes in nutrient content can be directly related to litter production, because the litter mass was significantly lower in the firebreak plots (0.207 kg/m<sup>2</sup>) than in control plots (0.366 kg/m<sup>2</sup>) ( $t_{27} = 3.92$ ,  $P < 0.01$ ) (Table 2). The high variability found can be attributed to differences in aspect, location and altitude, yet even so, we found significant differences.



**Fig. 3 – Species scores and plot scores in the ordination space defined by axis I and axis II of the DCA based on species densities. Polygons enclose the plots of the different sampling periods, solid lines for 1990 plots (circles), slashed lines for 2004 plots (squares) and dotted lines for control plots (triangles) (Eigenvalues of axes I and II were 0.238 and 0.097 and the cumulative percentage of variance of both axes was 35.3%). Species names are indicated with the first pair of letters of genus and species. Dagn, *Daphne gnidium*; Coca, *Convolvulus canariensis*; Erar, *Erica arborea*; Ersc, *Erica scoparia*; Glsa, *Globularia salicina*; Hygr, *Hypericum grandifolium*; Ilca, *Ilex canariensis*; Last, *Lavandula stoechas*; Lano, *Laurus novocanariensis*; Myfa, *Myrica faya*; Ptaq, *Pteridium aquilinum*; Prlu, *Prunus lusitanica*; Ruin, *Rubus inermis*; Smi, *Smilax* spp.; Sool, *Sonchus oleraceus*; and Viti, *Viburnum tinus* ssp. *rigidum*.**



**Fig. 4 – Species scores and plot scores in the ordination space defined by axis I and axis II of the DCA based on species biovolume. Polygons enclose the plots of the different sampling periods, solid lines for 1990 plots, slashed lines for 2004 plots and dotted lines for control plots (eigenvalues of axes I and II were 0.416 and 0.170 and the cumulative percentage of variance of both axes was 43.7%). Species names are indicated as in Fig. 3.**

#### 4. Discussion

In spite of the importance of vegetation monitoring in permanent plots (Bakker et al., 2002) and the fact that the laurel forest is probably the most characteristic ecosystem of the archipelago (Fernández-Palacios et al., 2004), this is the longest term study carried out in this plant community. Long-term studies offer very valuable information when studying the effects of disturbance because of the transient nature of the initial species responses (Tilman, 1988). Depending on the characteristics of the disturbance, that is, its extent, time, and magnitude (Glenn-Lewin and van der Maarel, 1992), the vegetation may show a response varying from resistance, via recovery with more or less complete return to the initial state,

**Table 2 – Selected chemical properties of the analyzed plots**

	Litter (kg/m <sup>2</sup> )	mg NO <sub>3</sub> <sup>-</sup>	mg NH <sub>4</sub> <sup>+</sup>	mg PO <sub>4</sub> <sup>2+</sup>	pH
Firebreak	0.207 (0.098)**	0.62 (0.99)*	23.91 (11.74)*	4.01 (1.39)*	6.5 (0.38) (ns)
Forest (control)	0.366 (0.055)	3.92 (5.39)	44.25 (19.84)	5.98 (2.42)	6.8 (0.07)

Mean values (standard error) of 23 samples for the plots in 2004 and 6 samples for the control plots. Significant differences among plots are indicated with an asterisk (for P < 0.05) or two asterisks (for P < 0.01; ns, non-significant).

**Table 3 – Logistic regression of the sampling period with respect to the sample scores along axis I and II (ns, non-significant)**

	Axis I – DCA base in biovolume			Axis II – DCA base in biovolume		
	Parameter B	Wald statistic	Significance level	Parameter B	Wald statistic	Significance level
1990–2004	1.22	0.663	ns	4.72	11.850	<0.01
Control–1990	8.79	4.402	< 0.05	0.630	0.046	ns
Control–2004	9.131	1.774	ns	4.365	0.610	ns

to irreversible changes (Collins et al., 2000; van de Koppel and Rietkerk, 2000).

Our results reveal that the vegetation structure (species richness, density and biovolume) in the firebreak differs from the control plots (especially the much higher biovolume of control plots). It can be argued that differences in species richness are due to the lower sampling effort, that is, number of control plots. However, the control plots were quite homogeneous (Appendix A) and increased sampling effort would not change the results significantly.

Nutrient content is significantly lower for nitrate, ammonium and available phosphorus in the firebreak plots than in the control plots in 2004. As long as these forests can be considered to be in a stable state (Fernández-Palacios et al., 1992), nutrient availability will be determined by litter production which is significantly lower in the firebreak and, hence, with less soil nutrients available for plant growth.

The DCA (based on densities) polygon comprising the control plots is located in the centre of the other polygons (Fig. 3), in an area of the ordination where woody species are dominant (*Laurus novocanariensis*, *Erica arborea*, *Erica scoparia*, *Myrica faya*, *Ilex canariensis*), while plots in 1990 can be characterized by specific species such as *Rubus inermis*, *Convolvulus canariensis*, *Lavandula stoechas* and in 2004 by *Smilax* sp., *Hypericum grandifolium* and *Sonchus oleraceus*. These species can be considered opportunistic and helophytic, appearing as important components of the vegetation in areas under other laurel forest disturbances such as fire (Arévalo et al., 2000) and canopy gaps (Arévalo and Fernández-Palacios, 1998).

Changes based on biovolume of species composition revealed significant differences in species composition between control plots and firebreak plots in both study periods. As in the DCA based on densities, the effect resulted in an increase in species heterogeneity in the plots due to the regular maintenance of the firebreak (a low intensity but continuous disturbance). Dominance in the tree biovolume and the low importance of the herbaceous layer discriminated the control plots from the firebreak plots at both periods (Appendix A).

#### 4.1. Management implications

Although temporal studies are greatly affected by temporal and spatial scales as well as by sampling design (Lepš and Rejmánek, 1991), analysis based on nutrient content, vegetation structure and species composition gave consistent results

in this study. After 20 years of succession, we can consider that the firebreak vegetation represents an early phase of the laurel forest found in the surrounding matrix but requiring recovery of biovolume and a reduction in shrubs and forbs species.

Although recovery is slow, we suggest that the area will reach a successional status of mature laurel forest due to several factors: the low intensity of the disturbance (spatial and temporal); a well-conserved surrounding matrix forest, offering a constant source of propagules from bird dispersion, as one of the characteristics of the laurel forest (Carvalho, 2002); and maintenance of species richness due to vegetative regrowth, which is very characteristic of the tree species of the laurel forest (Fernández-Palacios and Arévalo, 1998). Vegetative regeneration has been shown to be a very powerful mechanism for maintaining species richness following logging (Saulei and Lamb, 1990).

In order to accelerate succession, some imposed management can be suggested, such as the reduction of the number of basal sprouts resulting from tree coppicing in the firebreak. This would favour the development and growth of the canopy, providing more similar environmental conditions to the forest interior, increasing litter production and reducing opportunistic species richness. Furthermore, the opening of anthropogenic corridors (new roads or clearing) should be discouraged unless there are no other possible alternatives.

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#### Appendix A

The biovolume of each species per plot and year sampled is shown in Table A.1. Information for the control plots is also included. The density of each species per plot (16 m<sup>2</sup>) and year sampled is shown in Table A.2 along with information for the control plots.

Table A.1

	Coca	Dagn	Erar	Ersc	Glsa	Hygr	llca	Laaz	Laca	Myfa	Prlu	Ptaq	Ruin	Smi	Soca	Viti
p1-04	-	2.19	-	48.49	0.64	-	9.46	2.96	-	-	-	0.55	-	-	-	-
p2-04	-	1.94	-	34.79	4.86	-	-	-	-	11.18	-	0.95	-	-	-	-
p3-04	-	0.20	-	2.79	2.49	-	3.72	-	-	13.82	-	1.52	-	-	-	-
p4-04	-	9.90	2.00	25.78	4.32	-	12.53	1.49	-	9.65	-	2.15	-	-	-	0.15
p5-04	-	4.83	1.49	62.38	-	-	-	1.84	-	15.96	-	0.73	-	-	-	-
p6-04	-	1.27	-	37.14	0.92	-	1.83	3.34	-	11.36	-	4.78	-	-	-	15.53
p7-04	-	0.62	-	62.68	-	-	25.20	4.85	-	2.13	-	1.25	-	-	-	2.17
p8-04	-	13.29	-	55.55	-	-	15.76	8.98	-	11.60	-	0.73	-	-	-	2.26
p9-04	-	0.52	-	4.92	-	-	16.63	3.28	-	5.31	11.19	2.70	-	-	-	2.80
p10-04	-	6.79	-	1.74	-	-	53.29	2.44	-	-	-	16.29	-	-	-	0.19
p11-04	-	3.67	-	21.96	6.76	-	1.95	1.69	-	-	15.91	3.28	-	-	-	2.34
p12-04	-	0.65	4.00	31.14	5.19	-	33.19	1.24	-	3.83	-	1.33	-	-	-	0.61
p13-04	-	4.56	1.93	34.68	0.43	-	4.58	0.85	-	0.54	-	2.88	-	-	-	0.37
p14-04	-	2.69	-	32.93	0.77	-	1.48	0.62	-	6.43	-	1.43	-	-	-	0.17
p15-04	-	0.54	-	71.98	-	-	4.89	0.18	-	-	0.13	2.50	-	-	-	0.13
p16-04	-	-	-	9.34	-	-	14.67	0.23	-	-	-	9.99	-	-	-	3.14
p17-04	-	13.59	-	11.26	-	-	27.53	2.76	-	-	19.33	7.75	-	-	-	-
p18-04	-	3.59	-	52.42	-	-	58.36	0.48	-	-	3.66	21.97	-	-	-	29.26
p19-04	-	-	-	79.21	-	-	35.28	17.93	-	-	-	22.54	-	-	-	9.62
p20-04	-	-	-	37.44	6.65	-	5.96	0.50	-	-	-	1.21	-	-	-	1.62
p21-04	-	4.46	-	35.12	3.33	-	7.65	0.81	-	-	-	3.26	-	-	-	0.29
p22-04	-	0.13	-	15.60	0.63	-	17.29	0.16	-	-	2.36	3.23	-	-	-	3.31
p23-04	-	5.46	0.64	25.67	4.89	-	8.55	0.23	0.18	-	-	3.25	-	-	-	0.37
p1-90	-	1.14	1.72	6.89	0.43	0.16	1.82	0.25	-	1.44	-	1.33	-	-	-	-
p2-90	-	0.42	2.46	5.42	-	2.26	1.57	0.48	-	0.69	-	-	-	-	-	-
p3-90	-	0.77	1.23	5.94	-	-	0.98	0.25	-	2.24	-	-	-	0.77	-	-
p4-90	-	0.38	3.39	7.59	0.14	-	1.39	0.38	-	1.26	-	-	-	-	-	-
p5-90	-	1.33	7.26	3.74	0.33	-	3.48	0.73	-	4.49	-	-	-	-	-	-
p6-90	-	0.59	5.74	3.52	0.49	-	5.44	0.71	-	2.40	2.65	-	-	-	-	0.68
p7-90	-	3.19	2.23	5.12	-	-	6.39	0.74	-	2.26	-	-	-	-	-	0.62
p8-90	-	4.80	3.73	1.67	-	-	4.65	0.58	-	2.87	-	-	-	-	-	0.95
p9-90	-	0.95	1.44	2.28	-	-	3.84	0.14	-	0.42	3.19	-	-	-	-	-
p10-90	-	0.57	-	2.89	-	-	12.29	1.98	-	0.24	-	-	-	-	-	-
p11-90	-	-	-	1.28	0.86	-	12.24	0.21	-	-	-	-	-	-	-	0.90
p12-90	-	-	0.85	2.76	0.44	-	0.93	-	-	0.94	-	-	-	-	-	0.16
p13-90	-	-	0.36	4.75	0.19	-	0.67	0.48	-	0.38	-	-	-	-	-	-
p14-90	-	0.16	0.21	6.88	0.30	-	-	0.25	-	3.68	-	-	-	-	-	-
p15-90	-	-	-	9.52	-	-	0.68	-	-	0.25	-	-	-	-	-	-
p16-90	-	0.65	3.75	5.23	-	-	3.93	0.49	-	-	0.20	0.59	-	-	-	-
p17-90	-	0.12	-	2.65	-	-	9.78	0.14	-	-	11.64	6.27	-	-	-	-
p18-90	-	0.35	7.36	6.48	-	-	5.84	0.72	-	2.78	0.18	6.25	-	-	-	-
p19-90	-	0.80	0.16	3.46	1.37	-	6.32	-	1.40	-	0.77	1.12	-	-	-	0.91
p20-90	-	0.65	-	6.29	0.59	-	2.95	0.84	-	-	-	0.53	-	-	-	0.13
p21-90	-	0.83	0.25	1.64	0.48	-	14.98	0.93	-	0.53	-	-	-	-	-	0.70
p22-90	-	1.34	0.53	3.17	0.56	-	2.43	0.45	-	3.98	-	-	-	-	-	0.32
p23-90	-	0.14	9.48	1.25	-	-	7.43	0.52	-	-	0.96	1.54	-	-	-	0.12
c1	-	-	7.76	18.81	-	-	15.59	25.77	-	264.84	-	0.67	-	-	-	15.73
c2	-	-	-	47.99	-	-	32.84	0.34	-	11.38	-	0.59	-	-	-	17.63
c3	-	0.53	-	38.79	-	-	28.18	6.86	-	-	47.36	0.25	-	-	-	1.82
c4	-	-	-	32.49	-	-	-	1.85	-	481.17	74.51	0.58	-	-	-	0.48
c5	-	-	-	-	-	-	7.90	8.54	-	214.33	-	0.82	-	-	-	1.42
c6	-	-	15.14	92.73	-	-	3.78	74.69	-	47.92	-	-	-	-	-	-

Species names are indicated as in Fig. 3; bold type-face for tree species, italic for shrubs and roman for forbs.

Table A.2

	Coca	Dagn	Erar	Ersc	Glsa	Hygr	llca	Laaz	Laca	Myfa	Prlu	Ptaq	Ruin	Smi	Soca	Viti
P1-04	-	2	-	16	1	-	2	3	-	-	-	6	1	-	-	-
P2-04	-	4	-	16	2	-	-	-	-	5	-	1	-	-	-	-
P3-04	-	1	-	15	5	-	4	-	-	2	-	6	-	-	-	-
P4-04	2	8	2	14	5	-	7	2	-	4	-	9	-	-	-	2
P5-04	-	4	2	24	-	-	-	3	-	6	-	2	2	-	-	-
P6-04	2	1	-	6	1	-	2	3	-	1	-	11	1	-	-	4
P7-04	1	2	-	14	-	-	4	5	-	3	-	8	3	-	-	4
P8-04	-	3	-	13	-	-	5	16	-	1	-	6	-	-	-	1
P9-04	4	1	-	4	-	-	4	9	-	1	3	10	2	-	-	5
P10-04	-	2	-	1	-	-	8	6	-	-	-	39	1	-	-	5
P11 -04	4	2	-	4	3	-	6	6	-	-	7	15	2	-	-	10
P12-04	6	1	2	10	4	-	14	13	-	2	-	10	-	-	-	6
P13-04	3	5	2	24	2	-	7	7	-	1	-	18	-	-	-	4
P14-04	1	2	-	18	6	-	2	4	-	1	-	12	-	-	-	4
P15-04	11	1	-	22	-	-	7	2	-	-	2	16	-	-	-	5
P16-04	1	-	-	12	-	-	4	4	-	-	-	15	-	-	-	6
P17-04	2	1	-	7	-	-	6	4	-	-	9	9	6	-	-	-
P18-04	2	2	-	5	-	-	12	1	-	-	3	26	10	-	-	4
P19-04	1	-	-	4	-	-	8	4	-	-	-	17	17	-	-	4
P20-04	1	-	-	4	12	-	4	1	-	-	-	5	-	-	-	7
P21-04	2	2	-	5	20	-	4	8	-	-	-	11	-	-	-	6
P22-04	5	2	-	5	7	-	11	6	-	-	3	10	-	-	-	17
P23-04	2	3	1	9	13	-	8	9	6	-	-	21	-	-	-	14
P1-90	-	3	5	9	2	1	2	1	-	4	-	2	-	-	1	-
P2-90	-	4	1	7	-	1	2	1	-	4	-	-	-	-	-	-
P3-90	-	4	5	15	-	-	3	2	-	4	-	-	-	1	-	-
P4-90	-	3	9	20	3	-	6	3	-	7	-	-	-	-	-	-
P5-90	-	4	5	14	1	-	4	2	-	4	-	-	-	-	-	-
P6-90	-	5	4	7	1	-	7	5	-	2	3	-	-	-	-	2
P7-90	-	4	5	13	-	-	10	6	-	4	-	-	-	-	-	7
P8-90	-	7	3	6	-	-	6	6	-	1	-	-	-	-	-	4
P9-90	-	1	2	4	-	-	6	3	-	1	1	-	-	-	-	-
P10-90	-	4	-	2	-	-	11	6	-	2	-	-	-	-	-	-
P11 -90	-	-	-	8	4	-	10	2	-	-	-	-	-	-	-	7
P12-90	-	-	2	9	2	-	1	-	-	3	-	-	-	-	-	1
P13-90	-	-	1	6	2	-	1	1	-	1	-	-	-	-	-	-
P14-90	-	1	1	5	2	-	-	1	-	3	-	-	-	-	-	-
P15-90	-	-	-	4	-	-	3	-	-	1	-	-	-	-	-	-
P16-90	-	3	2	5	-	-	5	1	-	-	1	3	1	-	-	-
P17-90	-	2	-	1	-	-	6	1	-	-	3	5	1	-	-	-
P18-90	-	1	2	6	-	-	3	3	-	1	1	5	2	-	-	-
P19-90	-	1	1	3	4	-	5	-	2	-	4	4	-	-	-	3
P20-90	-	1	-	4	2	-	7	2	-	-	-	1	-	-	-	1
P21-90	-	2	1	2	3	-	5	3	-	2	-	-	-	-	-	2
P22-90	-	3	1	6	4	-	4	2	-	1	-	-	-	-	-	4
P23-90	-	2	2	2	-	-	4	4	-	-	2	5	-	-	-	1
C1	1	-	1	1	-	-	6	9	-	4	-	2	-	-	-	5
C2	-	-	-	4	-	-	5	9	-	2	-	5	-	-	-	6
C3	1	1	-	4	-	-	3	8	-	-	5	2	-	-	-	6
C4	-	-	-	4	-	-	-	7	-	1	2	1	-	-	-	1
C5	-	-	-	-	-	-	4	14	-	2	-	2	-	-	-	4
C6	1	-	1	7	-	-	3	8	-	2	-	-	-	-	-	-

Species names are indicated as in Fig. 3; bold type-face for tree species, italic for shrubs, and roman for forbs.

## REFERENCES

- Ancochea, E., Fuster, J.M., Ibarrola, E., Cendrero, A., Coello, J., Hernán, F., Cantagrel, J.M., Jamond, C., 1990. Volcanic evolution of the island of Tenerife (Canary Islands) in the light of new K-AR data. *Journal of Volcanic and Geothermal Research* 44, 231-249.
- Anon, 1973. Inventario forestal nacional. Ministerio de Agricultura, Pesca y Alimentación. S/C de Tenerife. Sección de inventario y mapas, Madrid.
- Arévalo, J.R., 1998. Organización Espacial y Temporal de la Laurisilva de Anaga Tenerife. Islas Canarias. PhD thesis, Universidad de La Laguna, La Laguna.
- Arévalo, J.R., Fernández-Palacios, J.M., 1998. Treefall gap characteristics and its influence on regeneration in the

- laurel forest of Tenerife. *Journal of Vegetation Science* 9, 297-306.
- Arévalo, J.R., Fernández-Palacios, J.M., 2003. Spatial patterns of trees and juveniles in a laurel forest in Tenerife, Canary Islands. *Plant Ecology* 165, 1-10.
- Arévalo, J.R., Fernández-Palacios, J.M., Palmer, M.W., 1999. Tree regeneration and future dynamics of the laurel forest on Tenerife, Canary Islands. *Journal of Vegetation Science* 10, 861-868.
- Arévalo, J.R., DeCoster, J.K., McAlister, S.D., Palmer, M.W., 2000. Changes in two Minnesota forests during 14 years following catastrophic windthrow. *Journal of Vegetation Science* 11, 833-840.
- Bakker, J.P., Elzinga, J.A., de Vries, Y., 2002. Effects of long term cutting in a grassland system: perspectives for restoration of plant communities on nutrient-poor soils. *Applied Vegetation Science* 5, 107-120.
- ter Braak, C.J.F., Šmilauer, P., 1998. *CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4)*. Microcomputer Power, Ithaca, NY.
- Carvalho, L., 2002. *Dinámica Temporal y Espacial de la Lluvia de Frutos en la Laurisilva (Anaga-Tenerife)*. Thesis graduation. Universidad de La Laguna, La Laguna.
- Collins, S.L., Micheli, F., Hartt, L., 2000. A method to determine rates and patterns of variability in ecological communities. *Oikos* 91, 285-293.
- Fernández-Palacios, J.M., Arévalo, J.R., 1998. Tree strategies regeneration of the trees in the laurel forest of Tenerife (The Canary Islands). *Plant Ecology* 127, 21-29.
- Fernández-Palacios, J.M., de los Santos, A., 1996. *Ecología de las Islas Canarias. Muestreo y análisis de poblaciones y comunidades*. Sociedad La Cosmológica, Santa Cruz de Tenerife.
- Fernández-Palacios, J.M., López, R., Luzardo, C., García, J., 1992. Descripción ecológica y evaluación de la producción primaria neta de cuatro estaciones representativas de los ecosistemas más característicos de Tenerife (Islas Canarias). *Studia Ecologica* 9, 105-124.
- Fernández-Palacios, J.M., Arévalo, J.R., Delgado, J.D., Otto, R., 2004. *Canarias, Ecología, Medio Ambiente y Desarrollo*. Centro de la Cultura Popular Canaria, S/C de Tenerife.
- Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematic* 29, 207-231.
- Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, A.J., Swanson, F.J., Turrentine, T., Winter, T.C., 2002. *Road Ecology: Science and Solutions*. Island Press, Washington, DC, USA.
- Franklin, S.B., Robertson, P.A., Fralish, J.S., Kettler, S.M., 1993. Overstory vegetation and successional trends of Land Between The Lakes, USA. *Journal of Vegetation Science* 4, 509-520.
- Gauch Jr., H.G., 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge, UK.
- Glenn-Lewin, D.C., van der Maarel, E., 1992. Pattern and processes of vegetation dynamics. In: Glenn-Lewin, D.C., Peet, R.K., Veblen, T.T. (Eds.), *Plant Succession: Theory and Predictions*. Chapman and Hall, London, pp. 11-59.
- Gurevitch, J., Padilla, D., 2004. Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution* 19, 470-474.
- Hamilton, L.S., Juvik, J.O., Scatena, F.N., 1995. The Puerto Rico tropical cloud forest symposium: introduction and workshop synthesis. In: Hamilton, L.S., Juvik, J.O., Scatena, F.N. (Eds.), *Tropical Montane Cloud Forests*. Ecological Studies, 110. Springer, New York, pp. 1-23.
- Hill, M.O., Gauch Jr., H.G., 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42, 47-58.
- Holl, K.D., Steele, H.N., Fusari, M.H., Fox, L.R., 2000. Seed banks of maritime chaparral and abandoned roads: potential for vegetation recovery. *Journal of the Torrey Botanical Society* 127, 207-220.
- Izquierdo, I., Martín, J.L., Zurita, N., Arechavaleta, M., 2001. *Lista de Especies Silvestres de Canarias. Hongos, Plantas y Animales*. Consejería de Política Territorial y Medio Ambiente, Gobierno de Canarias, S/C de Tenerife.
- van de Koppel, J., Rietkerk, M., 2000. Herbivore regulation and irreversible vegetation change in semi-arid grazing systems. *Oikos* 90, 253-260.
- Lepš, J., Rejmánek, M., 1991. Convergence or divergence: what should we expect from vegetation succession. *Oikos* 62, 261-262.
- Milberg, P., Lamont, B.B., 1995. Fire enhances weed invasion of roadside vegetation in Southwestern Australia. *Biological Conservation* 73, 45-49.
- Olsen, S.R., Cole, C.V., Watanabe, F.S., Dean, L.A., 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. US Department of Agriculture, Circular 939.
- Parsons, J.J., 1981. Human influence in the pine and laurel forest of the Canary Islands. *Geographical Review* 71, 253-271.
- Pickett, S.T.A., White, P.S., 1985. *The Ecology of Natural Disturbances and Patch Dynamics*. Academic Press, Orlando, FL.
- Santos, A., 1990. *Bosques de Laurisilva en la Región Macaronésica*. In: *Colección Naturaleza y Medio Ambiente*, No. 49. Council of Europe, Strasbourg.
- Saulei, S., Lamb, D., 1990. Regeneration following pulpwood logging in lowland rain forest in Papua New Guinea. In: Gómez-Pompa, A., Whitmore, T.C., Hadley, M. (Eds.), *Rain Forest Regeneration and Management. Man and the Biosphere Series*, Vol. 6. The Parthenon Publishing Group, Paris, pp. 313-322.
- Sims, G.K., Ellsworth, T.R., Mulvaney, R.L., 1995. Microscale determination of inorganic nitrogen in water and soil extracts. *Communications in Soil Science and Plant Analysis* 26, 303-316.
- Spellerberg, I.F., 1998. Ecological effects of roads and traffic: literature review. *Global Ecology and Biogeography Letters* 7, 317-333.
- SPSS, 1986. *SPSS/PC+V.6.0. Base Manual*. SPSS Inc, Chicago, IL.
- Switalski, T.A., Bissonette, J.A., DeLuca, T.H., Luce, C.H., Madej, M. A., 2004. Benefits and impacts of road removal. *Frontiers in Ecology and the Environment* 2, 21-28.
- Terradas, J., 2001. *Ecología de la Vegetación*. Omega, Barcelona.
- Tilman, D., 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, NJ.
- Zar, J.H., 1984. *Biostatistical Analysis*, second ed. Prentice-Hall, Englewood Cliffs, NJ.