

## The footprint of land use on the Macaronesian laurel forest landscape: an underestimated driving factor in protected areas

La huella de la actividad humana en el paisaje de la laurisilva macaronésica:  
un factor subestimado en las áreas protegidas

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### SUMMARY

Centuries of exploiting resources on Macaronesian islands left a significant footprint on their landscapes, even in areas where human activity would seem to be virtually absent. To clarify such interference, this paper explored how the impact of land use determined some attributes of current laurel forest landscape. Focused on communities dominated by heath and *Morella faya*, this work analyzed the effect of land use on their physiognomy and floristic composition, challenging the interpretation as climax communities. Based on a synchronic approach, the collected data supported a dynamic interpretation of such communities, installed on areas disturbed by human activities over long periods in the past. The combination of floristic composition, structure and land-use proxies suggested that such communities should be interpreted as subseral communities. This interpretation led to the idea that human factor should be considered as a critical driving force shaping landscape. Such an approach, promoting an adjustment in the scientific interpretation, assumed that current attributes of such communities were derived from past land-use options and do not represent a single response to abiotic conditions. Without questioning the value of those communities for conservation, that approach pointed out that protection measures should consider the potential occurrence of significant changes in terms of floristic composition and structure at medium term in that type of communities.

*Key words:* laurel forest dynamics, climax vegetation, human activity, disturbance, subseral communities.

### RESUMEN

La explotación de recursos forestales en las islas macaronésicas durante siglos ha dejado una notable huella en el paisaje, incluso donde no parece haber existido intervención humana. Para aclarar la intensidad de la interferencia antrópica, este trabajo analiza cómo el impacto de la actividad humana determinó algunos rasgos del paisaje actual de la laurisilva. Se estudian comunidades dominadas por brezo y *Morella faya* para conocer el efecto del uso del territorio en su composición florística, cuestionando su interpretación como comunidades climácicas. La información que se aporta fundamenta una interpretación dinámica de estos bosques, localizados en áreas explotadas durante siglos. La combinación de datos de composición florística y estructura con los del uso del suelo indica que estas comunidades deben ser consideradas como etapas de sustitución de las climácicas. Esta interpretación revela que la explotación antrópica debe ser considerada como un factor importante de la dinámica del paisaje. Este enfoque propone un cambio en la explicación científica, al reforzar la idea de que las características actuales de estos bosques no constituyen una respuesta exclusiva de las condiciones abióticas. Sin poner en cuestión su valor para la conservación, esta perspectiva defiende que las políticas de protección deben contemplar la posibilidad de que a medio plazo puedan ocurrir cambios importantes en la composición florística y la estructura de estas comunidades.

*Palabras clave:* dinámica de la laurisilva, vegetación climácica, actividad humana, perturbación, comunidades subseriales.

### INTRODUCTION

Scientific models about climax communities elaborated by botanists, ecologists and geographers have been very useful, nonetheless should be unceasingly tested from the new perspectives offered by the advancement of

knowledge and new techniques of analysis and interpretation of vegetation and landscape. More and more data are becoming available, allowing confirming that current plant communities have been radically transformed by human activity, both in their structure and floristic composition, as well as in their distribution. This is particularly important

today, with significant changes in uses and land cover happening (Mather 1990, Laforteza *et al.* 2008).

Until a few years ago, the dominant system of land use was based on less intensive although widespread interventions in the territory. The current trend is the abandonment of many agricultural, livestock and forest areas and intensification in more reduced spaces, namely for urban or agricultural uses. At the same time, the designation of protected areas creates a new context for landscapes that had been associated with specific land use and resources exploitation in the past. Since management is mostly oriented by conservation guidelines, it is important to assume that adjustments on the interpretation might be needed to cope with new and unknown dynamics, which are mainly determined by recovery at medium-long term.

In the studied area, Canary Islands and Madeira Island, it is commonly accepted that the summits of highest islands (> 2,000 m) have ecological conditions that promote the permanent installation of shrubby communities, very often dominated by legume shrubs (Tenerife: *Spartocytisus supranubii*; La Palma: *Genisto benehoavensis-Adenocarpum spartioidis*), which are replaced by hemicryptochamaephytic in dry supraoromediterranean areas (Tenerife: *Violetum cheiranthifolii*) (Del Arco *et al.* 2006). Below such altitudes, and limiting the analysis to areas potentially associated with evergreen laurel forests, excluding pine forests and thermomediterranean sclerophyllous woodlands, native shrubby communities are more commonly dominated by ericoid taxa. Some of such communities are interpreted to be subseral, and their hegemony is clear in significant areas of the landscape. This is the case of the Madeiran *Vaccinio padifolli-Ericetum maderinicolae* and *Globulario salicinae-Ericetum arboreae*, interpreted as subseral communities for the *Clethro arboreae-Ocoteo foetentis* and for the more humid version of the *Semele androgynae-Apollonio barbujanae* vegetation series respectively (Costa *et al.* 2012). For the Canaries, a similar interpretation is suggested for some forest expressions included in “fayal-brezal” (*Myrico fayae-Ericetum arboreae*), considered as subseral for the laurel forest, and resulting from its disturbance (Del Arco *et al.* 2006). Exception to rocky crests, where such communities, dominated by ericoid taxa, might establish permanently, exhibiting a floristic adjustment (Costa *et al.* 2004, Figueiredo and Sequeira 2010). While the interpretation as subseral or permanent communities seems to be adjusted, considering past land use dynamics and described abiotic conditions respectively, that is not the case for some communities that have been interpreted as climax and are dominated by *Erica arborea* L. (Madeira Island: *Polysticho falcinelli-Ericetum arboreae*), by *Erica platycodon* (Webb *et Berthel.*) Rivas Mart. *et al.* (Canaries: *Ilici canariensis-Ericetum platycodonis*) or by *Morella faya* (Ait.) Wilbur, before *Myrica faya* Aiton (Canaries: *Pericallido murrayii-Myricetum fayae*).

The interpretation of such communities as climax formations assumes that their traits reflect an equilibrium

with environmental conditions, ignoring the effect of different types of disturbance related to historical human activities and changes on land use patterns in association with different economic contexts. Previous results from the Canarian laurel forest suggested that different types of disturbance associated with land use along centuries promoted deep impacts in its coverage, structure and composition (Arozena 2005, Arozena *et al.* 2008, 2009, 2016, 2017, Rivero *et al.* 2010, Afonso *et al.* 2010, 2018, Arozena and Panareda 2013, Panareda *et al.* 2013). From this perspective, this paper has as principal goal to explore how current structure and floristic composition of specific communities, which have been interpreted as climax, reflect past land use. More than accepting current traits as static or expected for long-term, an assumption associated with the climax concept, collected data supports the idea that such attributes often represent drifts in succession, determined by variations in the intensity, duration and type of human activity, suggesting that changes at medium term could occur. The interference of forest resources exploitation as key driver to shape certain aspects of the structure, floristic composition and dynamics of communities typified by heath (*Erica arborea*, *Erica platycodon*) and *Morella faya* is discussed to support such hypothesis.

Considering that the presence of those communities was a strong argument to assign protection to some areas, the change in interpretation assumed in this article does not intend to challenge such status, its only aim is to provide additional information that might promote adjustments on conservation plans, considering potential changes on that type of communities at medium term.

## METHODS

The analysis carried out in this paper was based on a synchronic approach, nevertheless it also considered results from studies about life strategies of tree species and their effects on the structure of the laurel forest during more than 30 years. This knowledge has provided the basis to extract information about its dynamics through the comparison of different types of current forest.

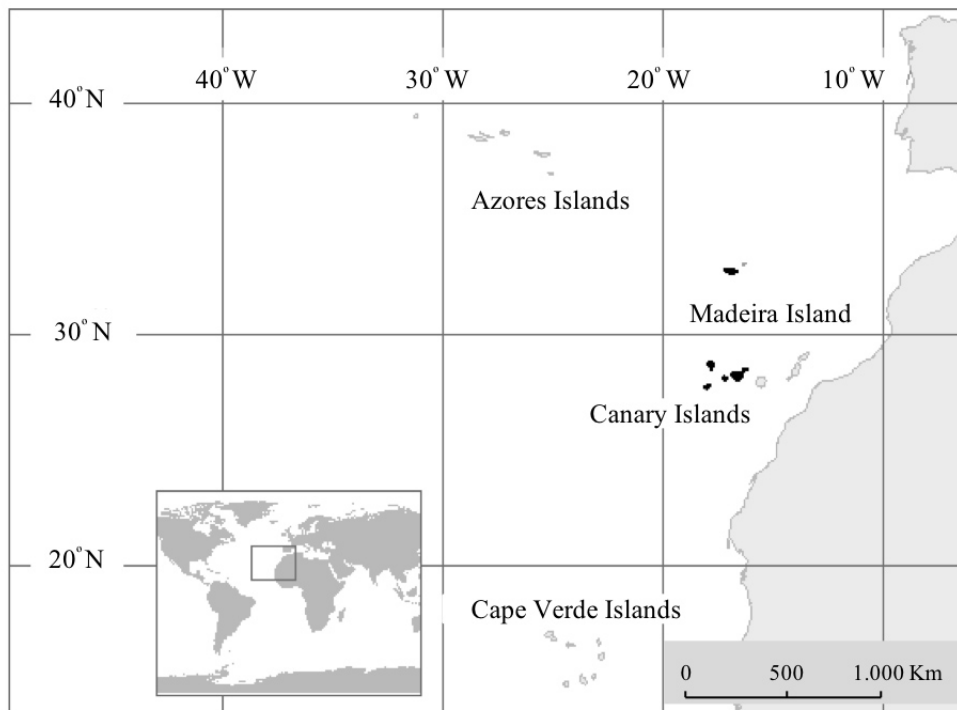
The structural characterization of the studied communities, as well as their spatial relationship, was studied using the following techniques: (i) chorology of plant taxa at a 1x1 km scale (Arozena and Panareda 2014); (ii) phytosociological inventories (Braun-Blanquet 1964); (iii) profile-diagrams, to explore relationships between topography and the distribution of communities (Arozena *et al.* 2008, 2017). To know the dynamic meaning of each forest type (iv) forest inventories were used, complementing phytosociological inventories for demographic analysis/species and analysis of reproductive strategies/species (Arozena 2005); (v) graphic cross-section of the forest (Arozena *et al.* 2017), to reveal the circumstantial relation between the dominant species and differences in the height

and vertical structure of communities. The relationship of forest features with historical land uses was based on (vi) inventory and location of remains - charcoal production sites, buildings... - related to agricultural, livestock and forest exploitation within the current forest area (Arozena *et al.* 2008). (vii) Aerial photo interpretation was used to recognize trends of forest landscape change, comparing photograms of different time periods in the second half of the 20<sup>th</sup> century (Arozena *et al.* 2008). Syntaxonomy was based on Costa *et al.* (2004, 2012) and Del Arco *et al.* (2006).

*Study area.* Results were based on data collected on two islands of the western Canaries - El Hierro and Tenerife - and on Madeira Island (figure 1). These areas were selected for this study based on the fact that they share geographical attributes and vegetation features: all islands are of volcanic origin, present significant altitudinal gradients, exhibit a clear climatic asymmetry between their drier leeward-southern faces and their more humid windward-northern faces, due to the trade winds, and a climatic pattern that clearly reflects the great importance of the Azores High. Despite climatic similarities, Madeira Island registers higher values of annual precipitation, since it is more exposed to the influence of low-pressure systems and less exposed to the influence of the desert. In fact, just small areas along the coast of the island are classified as dry inframediterranean (Capelo *et al.* 2004).

On the contrary, significant areas of the Canarian Islands register low values of precipitation, presenting values for annual precipitation under 200 mm - at lower altitudes on the southern face that are far below the minimum registered on Madeira Island - around 600 mm -. Differences in average annual temperature are larger within islands than among islands, a pattern clearly structured by significant altitudinal gradients (table 1).

Despite climatic differences, there are significant affinities in terms of flora and vegetation among the islands under study: they share a weighty number of taxa and contain plant communities with similar structure, floristic composition and life forms. This idea is particularly supported by the evergreen laurel forest, a type of vegetation generally associated with trade wind-facing slopes, where it benefits from additional water input or lower values of evapotranspiration due to the high frequency of cloud banks, especially during summer (Marzol-Jaén *et al.* 2010, Figueiredo 2013). Because of higher values of annual precipitation, potential vegetation at Madeira Island is mostly associated with laurel forests. Other types of vegetation are scarcely represented, such as dry scrub and sclerophyllous formations well represented in the Canaries. Other differences are related to the presence of native pine forests in the Canaries, dominating significant areas of the islands (Del Arco *et al.* 2006); and, because of the higher altitudinal gradients at some Canary Islands, the presence of cacuminal vegetation at the summits (Tenerife: *Spar-*



**Figure 1.** Location of the islands considered in this study (in black).

Localización de las islas consideradas en el presente estudio (en negro).

**Table 1.** Geographical attributes for studied islands.

Características geográficas de las islas estudiadas.

Archipelago	Island	Maximum altitude (m)	Site	Altitude (m)	Position	Prec. (mm)	T (°C)	TMax (°C)	TMin (°C)
Madeira	Madeira	1,862	Bica Cana	1,560	Sm	2,967	9.3	12.9	5.6
			Santana	380	N	1,442	15.2	17.8	12.7
			Lugar de Baixo	15	S	655	19.7	22.7	16.2
Canaries	Tenerife	3,718	Izaña	2,371	Sm	392	10.2	14.1	6.4
			Los Rodeos. TNA	632	N	520	16.8	20.5	13.0
	Sta. Cruz Tenerife	35	S	226	21.5	24.6	18.4		
	El Hierro	1,500	San Andrés	1,115	Sm	704	-	-	-
			Aeropuerto	33	S	206	21.1	23.3	18.7
			Sabinosa-Llanos	20	N	119	-	-	-

Site: TNA: Tenerife Norte Aeropuerto; Position: Sm = summits, N =North, S = South. Prec.: annual average precipitation (mm); T: annual average temperature (°C); TMax: average of annual maximum temperature (°C); TMin: average of annual minimum temperature (°C). Climatic data sources: AEMET (Spain) and IPMA (Portugal).

*toctisetum supranubii*, *Violetum cheiranthifoliae*) (Del Arco *et al.* 2006). These types of vegetation are absent on islands whose summits are under 2,000 m.

Moreover, such islands have been subjected to similar land use patterns during the last five hundred years, promoting the development of communities whose attributes exhibit the impacts from such disturbance.

## RESULTS

*Erica platycodon scrubland of Anaga Rural Park (Tenerife. Canary Islands).* In Anaga Rural Park (figure 2) a large part of the current forest area was occupied by scrublands whose canopy almost exclusively contained *E. platycodon*. This heliophilous species tolerates very windy areas and discontinuous and shallow soil.

In general, it consisted of a relatively tall *E. platycodon* shrubby community, very dense at its base and with a relatively closed canopy. It was organized in a moderately uniform mosaic of different facies that had a series of common traits:

- (i) The homogeneity of canopies within different sectors. One of the general traits of this scrub was the regularity of the height of canopy in each area. Canopy was only slightly broken by the emergence of occasional young specimen of *Ilex canariensis* Poir or, more frequently, dispersed old specimens of *Morella faya*.
- (ii) Within such community, all of the reproduction of *E. platycodon* was asexual and presented a homogenous physiognomy, as all specimens were multi-trunked at the base and new outbreaks presented a marked similarity in diameter.
- (iii) No seedlings or saplings of this species were found

in the understory. There was only evidence of sexual reproduction of *E. platycodon* on the edges of paths and in clearings of a certain size.

- (iv) There was always at least one generation of broad-leaved trees growing in the shade of the canopy. The density of the community seemed to be increasing by an abundance of young specimens of broad-leaved trees, especially *Laurus novocanariensis* Rivas-Martínez *et al.*, *Ilex canariensis* and *Viburnum rigidum* Vent.

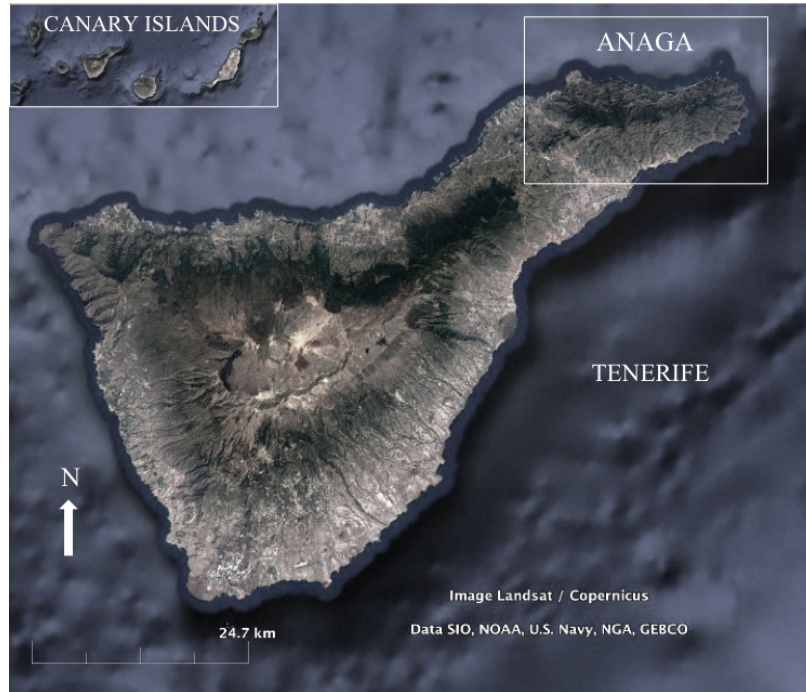
From this common base, variants (table 2) were considered based on differences on the height of the scrub, on the diameter of the stems of *E. platycodon*, on the proportion of broad-leaved trees, on the different sizes of young specimens, and on variations in the floristic composition of seedling and sapling levels (figure 3).

The edges of these scrublands were always very sharp. This precision in the change of plant physiognomy was not due to changes in the topography or in the soil characteristics; instead, their limits were coincident with the presence of forest trails and paths. Furthermore, it was observed that the dominance of a shape associated with asexual reproduction of *E. platycodon* was spatially coincident with the existence of charcoal piles (*carboneras*), recognizable by their particular shape and by remains of charcoal on the surface and at the upper levels of the soil. In addition, the comparison of aerial photographs taken at different moments in time showed a clear transformation of vegetation on the summits of Anaga over the past few decades (figure 4).

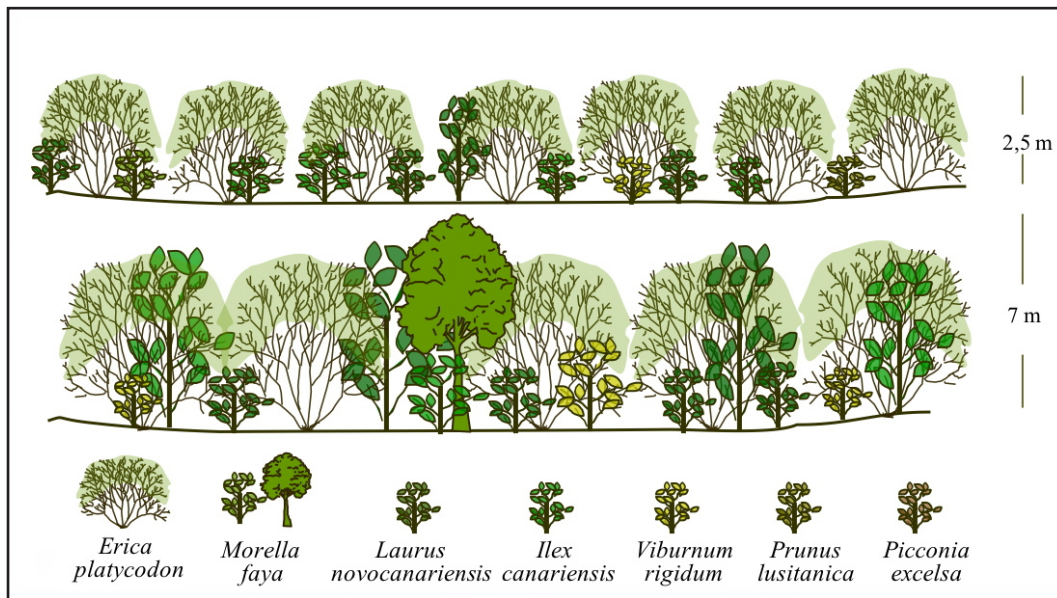
*Tree heath community on the summits of Madeira Island (Madeira Natural Park).* Tree heath -*Erica arborea*- is

found all over Madeira Island, ranging from coastal areas to the highest peaks of the island. Communities that integrate this taxon are usually interpreted as subseral of laurel forests (Capelo *et al.* 2004, Costa *et al.* 2012). It

is the case for *Globulario salicinae-Ericetum arboreae*, related to the more humid version of *Semele androgynae-Apollonio barbujuanae sigmetum*, and the *Vaccinio padifolii-Ericetum maderinicolae*, associated with *Clethro*



**Figure 2.** Location of Anaga Rural Park.  
Localización del Parque Rural de Anaga.



**Figure 3.** Different manifestations of *Erica platycodon* scrub in Anaga Rural Park.  
Distintas expresiones del matorral de *Erica platycodon* en el Parque Rural de Anaga.

*arboreae-Ocoteo phoetentis sigmetum*. This taxon also integrates communities interpreted as permanent when occupying windy crests with poor soils (Capelo *et al.* 2004, Costa *et al.* 2012). Nonetheless, at altitudes above 1,500 m (figure 5), under hyper-humid to ultra-hyper-humid mesotemperate conditions, *Polysticho falcinelli-Ericetum arboreae*, a community dominated by this taxon

is interpreted as a climax, or at least a disclimax stage (Capelo *et al.* 2004, Costa *et al.* 2012).

The most significant feature of this community was the clear hegemony of two species highly heliophilous (*Erica arborea* and *Pteridium aquilinum*) (figure 6). Despite the paucispecific condition of such community, which presented high physiognomic and floristic homogeneity (table 3),

**Table 2.** Floristic composition of communities of *Erica platycodon* in Anaga Rural Park (Arozena *et al.* 2008).

Composición florística de las expresiones de *Erica platycodon* en el Parque Rural de Anaga (Arozena *et al.* 2008).

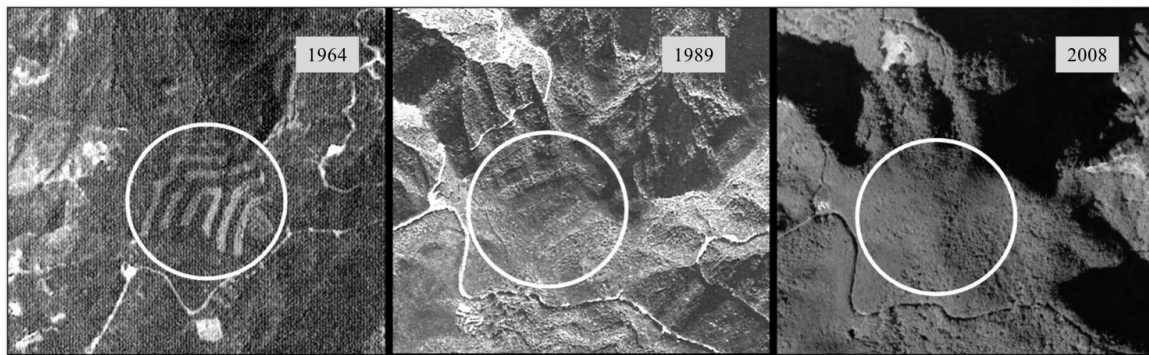
Inventory nº	1	2	3	4	5	6	7	8
Altitude (m)	910	970	760	860	690	780	870	810
Aspect	SSE	NE	NNW	SW	SSW	NNE	SE	W
Slope (°)	20	45	45	25	25	45	20	25
Area (m <sup>2</sup> )	75	70	50	80	50	35	100	20
Tree layer (%)	90	100	95	80	75	95	100	85
Shrub layer (%)	-	2	-	1	15	5	-	-
Herbaceous layer (%)	15	5	5	30	25	80	5	75
<i>Erica platycodon</i> (Webb <i>et</i> Berthel.) Rivas-Mart. <i>et al.</i>	3.3	5.5	4.4	3.4	4.4	5.5	4.4	5.5
<i>Ilex canariensis</i> Poir.	+	2.2	+	2.2	1.1	+	2.2	+
<i>Morella faya</i> (Aiton.) Willbur.	2.1	+	2.1	2.2	1.1	+	2.2	+
<i>Viburnum rigidum</i> Vent.	2.3	1.1	-	3.4	2.3	2.2	2.2	1.2
<i>Laurus novocanariensis</i> Rivas-Mart. <i>et al.</i>	1.2	2.1	2.3	2.2	2.2	2.2	3.4	3.4
<i>Prunus lusitanica</i> (Willd.) Franco	1.1	+	1.1	-	-	-	1.1	2.2
<i>Erica arborea</i> L.	2.1	-	-	-	-	-	-	-
<i>Picconia excelsa</i> (Aiton) DC.	1.1	-	-	-	-	-	-	-
<i>Heberdenia excelsa</i> (Aiton) Banks <i>ex</i> DC.	+	-	-	-	-	1.2	-	2.2
<i>Ilex platyphylla</i> (Webb <i>et</i> Berthel.) Tutin	-	-	+	-	-	-	-	-
<i>Phyllis nobla</i> L.	-	+	-	-	1.2	-	-	-
<i>Rubus ulmifolius</i> Schott	-	+	-	-	-	+	-	-
<i>Rubus bollei</i> Focke	-	-	-	+	-	-	-	+
<i>Aichryson laxum</i> (Haw.) Bramwell	-	1.2	-	-	-	-	-	-
<i>Hypericum grandifolium</i> Choisy	-	-	-	1.1	+	1.1	-	-
<i>Sonchus</i> sp	-	-	-	-	+	-	-	-
<i>Aeonium urbicum</i> (C. Sm. <i>ex</i> Buch) Webb <i>et</i> Berthel.	-	-	-	-	2.3	-	-	-
<i>Galium scabrum</i> L.	-	-	-	1.1	1.2	+	-	-
<i>Luzula</i> sp	-	+	-	-	-	-	-	-
<i>Ixanthus viscosus</i> (Sm.) Griseb.	-	-	-	-	+	+	-	-
<i>Pteridium aquilinum</i> (L.) Kuhn <i>in</i> Kerst	2.3	-	+	3.3	1.1	-	1.1	+
<i>Asplenium onopteris</i> L.	-	1.1	1.1	1.1	1.1	+	+	1.1
<i>Dryopteris oligodonta</i> (Desv.) Pic.-Serm	-	-	-	-	+	2.2	-	2.2
<i>Davallia canariensis</i> (L.) Sm.	-	-	+	-	1.1	+	-	-
<i>Polypodium macaronesicum</i> A. E. Bobrov	-	-	-	-	+	-	-	-
<i>Polystichum setiferum</i> (Forssk.) Moore <i>ex</i> Woynt.	-	-	-	-	+	-	-	-
<i>Asplenium hemionitis</i> L.	-	-	-	-	+	-	-	-
<i>Woodwardia radicans</i> (L.) Sm.	-	-	-	-	-	3.2	-	4.4
<i>Hedera canariensis</i> Willd	-	2.3	-	-	-	-	-	4.4
<i>Semele androgyna</i> (L.) Kunth	1.1	-	-	-	-	-	-	-
<i>Smilax canariensis</i> Willd.	+	-	-	-	+	-	-	+

From this common base, variants (table 2) were considered based on differences on the height of the scrub, on the diameter of the stems of *E. platycodon*, on the proportion of broad-leaved trees, on the different sizes of young specimens, and on variations in the floristic composition of seedling and sapling levels (figure 3).

broad-leaved taxa (*Ilex perado* Aiton, *Laurus novocanariensis*) were found quite often in areas surrounding sites where phytosociological inventories were collected, usually on steep slopes (table 3, inventories 1, 2 and 4). Once again, such a condition could indicate that floristic composition was exhibiting the result of a more intensive level of disturbance.

In most of the visited sites the shrub presented a multi-trunk structure (figure 6), suggesting the existence of a disturbance that favored asexual reproduction, a response very often associated with fire and cutting. This was clearly demonstrated by the significant and rapid recovery of *E. arborea* in areas where grazing was banned after 2003. On such areas, germination was clearly more dominant

than resprouting, a response not found in other native shrubs associated with this type of community. However, the vitality exhibited was not homogeneous over the entire area affected by grazing. In fact, it was much more vigorous in less-accessible areas with more pronounced slopes than in flat sectors, a pattern probably related to differences in grazing intensity. Curiously, many of the sites where these communities were described were located at the edges of large areas associated with grazing, probably also subjected to higher pressure during a certain period in the past. The vigorous response of *E. arborea* in areas where grazing was currently interdicted revealed the importance of such strategy to determine the physiognomy and floristic composition of a community after a distur-



**Figure 4.** Gradual change in the *Erica platycodon* scrub landscape on Anaga (Arozena *et al.* 2008). Source: TFA. Flight 1:30.000 in 1964 and flight 1:18.000 in 1989 and GRAFCAN 2008.

Cambio gradual del paisaje de los matorrales de *Erica platycodon* en el Parque Rural de Anaga (Arozena *et al.* 2008). Fuente: TFA (vuelo 1:30.000 de 1964 y vuelo 1:18.000 de 1989) y GRAFCAN 2008.

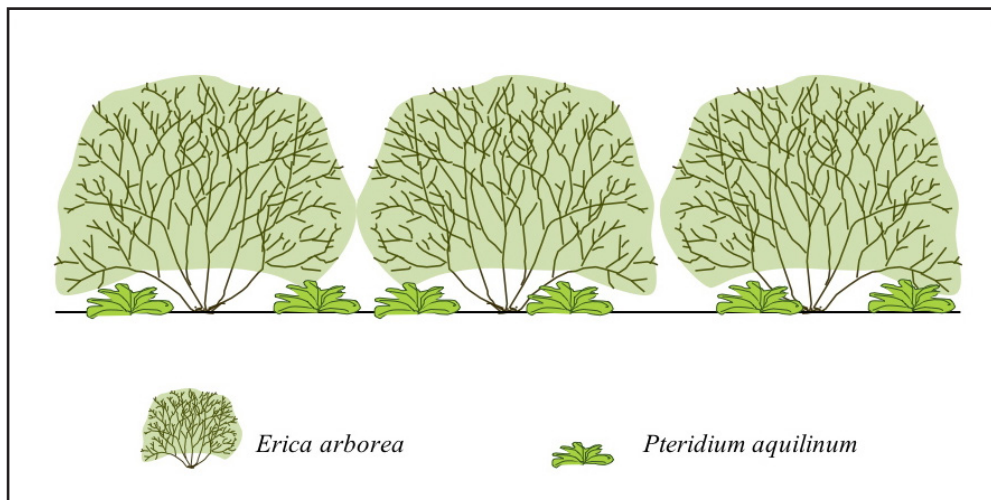


**Figure 5.** Location of the study area in Madeira Natural Park.

Localización del área de estudio en el Parque Natural de Madeira.

bance. The attributes of this type of community could also be due to the combined effect of the lack of propagules for other shrub/tree taxa in the seed bank, caused by extirpation after negative selection. The combination of these factors could be more important than expected, masking the real attributes of a community that might establish in such areas in the long term without disturbance.

*The Morella faya and Erica arborea forest in Frontera Rural Park (El Hierro, Canary Islands).* Another example that supported the idea of considering communities dominated by *E. arborea* and *M. faya* as subseral could be found in El Hierro Island. Mature laurel forests were scarcely represented on the island, even in the Frontera Rural Park (figure 7), whose landscape was generally do-



**Figure 6.** Forest section of Bica da Cana heath. Madeira Natural Park (table 3, inventory 4).  
Sección forestal del brezal de Bica da Cana. Parque Natural de Madeira (cuadro 3, inventario 4).



**Figure 7.** Location of the study area in Frontera Rural Park.  
Localización del área de estudio en el Parque Rural de Frontera.



**Table 3.** Floristic composition of *Erica arborea* communities on the summits of Madeira Island.

Composición florística de comunidades de *Erica arborea* en las cumbres de la Isla de Madeira.

Inventory nº	1	2	3	4	5	6
Altitude (m)	1,410	1,360	1,680	1,554	1,460	1,556
Aspect	NE	N	SE	NE	NE	NE
Slope (°)	20	30	45	5	-	-
Area (m <sup>2</sup> )	70	100	100	100	100	200
Tree layer (%)	80	95	90	95	-	-
Shrub layer (%)	5	-	-	-	-	-
Herbaceous layer (%)	10	5	5	50	-	-
<i>Erica arborea</i> L.	4.4	5.5	5.5	5.5	5	3
<i>Polystichum falcinellum</i> (Sw.) C. Presl	-	+	2	-	1	1
<i>Ranunculus minor</i> Lowe	-	+	-	-	1	+
<i>Erica maderinicola</i> D.C. McClint.	2.1	2.1	-	-	+	+
<i>Viola riviniana</i> Rechb.	+	+	+	1	1	1
<i>Sibthorpia peregrina</i> L.	+	+	+	-	1	+
<i>Ilex perado</i> Aiton	-	-	-	-	-	2
<i>Teucrium francoi</i> M. Seq., Capelo, J.C. Costa et R. Jardim	-	-	-	-	-	2
<i>Laurus novocanariensis</i> Rivas-Mart. et al.	-	-	-	-	-	1
<i>Vaccinium padifolium</i> Sm.	-	+	-	+	2	4
<i>Asplenium onopteris</i> L.	-	-	+	-	+	-
<i>Polystichum setiferum</i> (Forssk.) Moore ex Woyn.	+	+	+	-	+	+
<i>Brachypodium sylvaticum</i> (Huds.) P. Beauv.	+	+	-	+	1	-
<i>Blechnum spicant</i> (L.) Roth	+	-	+	-	-	-
<i>Bupleurum salicifolium</i> R. Br. ex Buch	-	+	+	-	+	1.1
<i>Rosa</i> sp	-	+	-	-	+	-
<i>Cedronella canariensis</i> (L.) Webb et Berthel.	-	+	-	-	-	+
<i>Agrostis castellana</i> Boiss. et Reut.	+	+	+	2.2	-	1
<i>Pteridium aquilinum</i> (L.) Kuhn	2.2	2.2	+	2.2	2	2
<i>Cardamine hirsuta</i> (L.)	-	-	-	-	-	2
<i>Cystopteris viridula</i> (Desv.) Desv.	-	-	-	-	+	2
<i>Origanum virens</i> Cout.	+	-	+	-	-	-
<i>Clinopodium arundanum</i> (Boiss.) Nyman	+	+	-	-	-	-
<i>Cerastium glomeratum</i> Thuill.	-	+	+	+	-	-
<i>Teesdalia nudicaulis</i> (L.) R. Br.	-	+	+	-	-	-
<i>Umbilicus rupestris</i> (Salisb.) Dandy	-	+	+	-	-	+
<i>Holcus lanatus</i> L.	-	+	-	+	-	-
<i>Carex lamprocarpa</i> Čelak.	-	-	-	+	-	+
<i>Rumex acetosella</i> L.	-	-	-	+	-	+
<i>Potentilla anglica</i> Laichard.	-	-	+	+	-	-
<i>Cytisus scoparius</i> (L.) Link	1	+	+	+	+	-
<i>Argyranthemum pinnatifidum</i> (L.f.) Lowe	+	-	+	-	-	-
<i>Hypochaeris radicata</i> L.	+	+	-	+	-	-

Inv. 1 (Paul da Serra): *Tolpis* sp +, *Sonchus fruticosus* L.f. +, *Duchesnea indica* (Andrews) Focke +, *Clethra arborea* Aiton +, *Sonchus* sp +; Inv. 2 (Ribeira do Alecrim): *Brixa maxima* L. +, *Aira caryophylla* L. +, *Veronica persica* Poir. +, *Leontodon* sp +; Inv. 3 (Pico Ruivo): *Dactylis* sp +, *Berberis maderensis* Lowe +, *Senecio sylvaticus* L. +, *Leontodon* sp +; Inv. 4 (Bica da Cana): *Hypericum humifusum* L. +, *Prunella vulgaris* L. +, *Taraxacum* sp +, *Pinus* sp +; Inv. 5 (Chão Lagoa): *Rubus suspiciosus* Menezes +, *Polypodium macaronesticum* Bobrov 1, *Polypodium macaronesticum* x *cambricum* (A.V. Brobov) Fraser-Jenk. +; Inv. 6 (Bica da Cana): *Andryala varia* Lowe ex D.C. +, *Hypericum undulatum* Schousbe ex Willd. +, *Polypodium cambricum* L. +, *Thymus micans* Lowe +. Inv. 5 and 6: Costa et al. 2004.

minated by communities of *M. faya* and *E. arborea*. Even on areas where the tree layer was dominant, the structure of the forest, the diameter of the trunks, and the walls related to agriculture fields, pointed to a recent recovery of vegetation after disturbance. A very interesting example was found at windward and leeward summits at the highest sector of the park, where the community dominated by *M. faya* is interpreted as climax (Del Arco *et al.* 2006).

On steep windward slopes, the forest was dominated by young multi-trunk specimens of *M. faya* -the trunks diameter had a 20 cm at breast height-, and, to a lesser degree, it also contained single-trunk *E. arborea* (table 4, inventory 4; figure 8, section III). On the flat leeward summits, *M. faya* still dominated (table 4, inventory 1), although the structure of the forest was very different: the specimens of such species were very old, with crowns developing horizontally from below half of their height, forming a relatively compact canopy, despite the small number of trunks. Just as on the windward side, there was no shrub layer and no young specimens of tree species, making it a closed forest at the canopy layer, but very open at the understory, where

there was only a continuous cover of the nitrophilous *Urtica morifolia* Poir (figure 8, section I). On few locations the age of *M. faya* was variable, a fact reflected in the physiognomy of the forest (table 4, inventory 3). A younger forest established a mosaic with multi-trunked heath specimens (*E. arborea*) (figure 8, section II), with a very important decrease in cover for *U. morifolia*, which was dominant in forests with higher cover of *M. faya* (table 4, inventory 2).

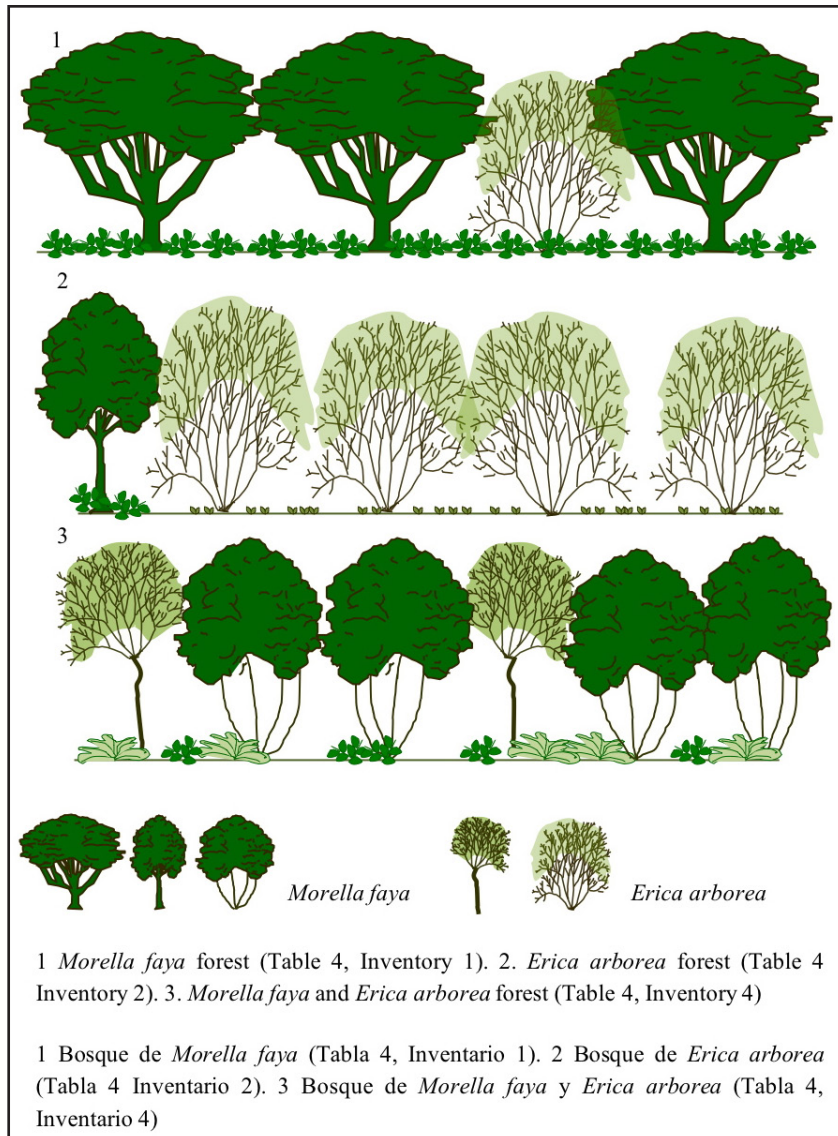
## DISCUSSION

The interpretation of the studied communities as climax is usually based on the presence of homogeneous formations regarding structure and floristic composition across significant areas, and sometimes extended to ridge-crest and summit macrophanerophytic communities, usually dominated by ericoid taxa. Nonetheless such homogeneity, very often accepted as only determined by abiotic conditions, was above all the response to particular types of exploitation of forest resources, charcoal production for instance.

**Table 4.** Floristic composition of *Morella faya* and *Erica arborea* communities on the summits of El Hierro Island.

Composición florística de las comunidades de *Morella faya* y *Erica arborea* en las cumbres de la Isla de El Hierro.

Inventory nº	1	2	3	4
Altitude (m)	1,337	1,328	1,348	1,203
Aspect	SSE	SE	SE	NW
Slope (°)	7	10	5	35
Area (m <sup>2</sup> )	100	100	80	100
Tree layer (%)	90	80	90	85
Herbaceous layer (%)	100	45	90	70
<i>Morella faya</i> (Aiton.) Willbur.	5	+	5	4
<i>Erica arborea</i> L.	1	5	1	2
<i>Urtica morifolia</i> Poir.	5	+	5	3
<i>Myosotis latifolia</i> Poir.	+	3	+	1
<i>Parietaria debilis</i> G. Forst.	+	1	+	+
<i>Micromeria</i> sp	+	-	-	-
<i>Davallia canariensis</i> (L.) Sm.	r	-	-	-
<i>Dryopteris oligodonta</i> (Desv.) Pic-Serm	+	-	+	3
<i>Pericallis murrayi</i> (Bornm.) B. Nord.	1	-	-	r
<i>Ranunculus cortusifolius</i> Willd.	r	-	-	-
<i>Drusa glandulosa</i> (Poir.) H. Wolff ex Engl.	+	+	-	-
<i>Carduus</i> sp	+	-	-	-
<i>Geranium purpureum</i> Vill.	-	+	+	+
<i>Brachypodium sylvaticum</i> (Huds.) P. Beauv.	-	r	-	-
<i>Galium scabrum</i> L.	-	+	-	-
<i>Sonchus</i> sp	-	r	-	-
<i>Asplenium onopteris</i> L.	-	-	-	r
<i>Aichryson laxum</i> (Haw.) Bramwell	-	-	-	+



**Figure 8.** Forest sections of the most contrasting manifestations of La Llanía forest.

Secciones forestales de las expresiones más contrastadas del bosque en La Llanía.

*Erica platycodon* communities associated with ridge crests submitted to year-round windy and cloudy conditions have been interpreted as a climax stage on the summits of Anaga (Tenerife) and La Gomera: *Ilici-Ericetum platycodonys* (Fernández-Palacios and Arévalo 1998, Arévalo *et al.* 1999, Del Arco and Wildpret 1999, Del Arco *et al.* 2006, Ohsawa *et al.* 2010, Rivas- Martínez 2009). Nevertheless, the gradual abandonment of traditional uses since the second half of the 20<sup>th</sup> Century (figure 4) had unleashed spontaneous forest dynamics that already showed enough signs to suggest an alternative explanation for current characteristics and distribution in Anaga. The form of *E. platycodon* specimens, indicative of disturbances that have favored asexual reproduction, and their current vertical structure, allowed assuming that the dominance of this

taxon and the characteristics of the scrub were the result of anthropic disturbance sustained over time.

The production of plant charcoal has been one of the main economic activities for farmers in Anaga for centuries (Rivero *et al.* 2010). Since the end of the 19<sup>th</sup> Century, the increasing need for this product in domestic use in the growing urban society led to the establishment of a large number of clandestine charcoal piles, where trails facilitated transporting the finished product to urban areas. The highest quality charcoal produced from *E. platycodon* contributed to promote its dominance in the landscape, which was the product of short-rotation (5 years) clear-cutting to produce plant charcoal (Rivero *et al.* 2010). This activity favored the development and maintenance of the main resource in detriment to other species, by paralyzing the

dynamics of the most heliophilous forest phase. Once this exploitation ceased, broadleaf species began to spontaneously develop in the shade of *E. platycodon*, indicating that without this kind of economic activity the forests at the summits would have more diverse flora and *E. platycodon* would be less dominant among the macrophanerophytes. In fact, the comparison of current floristic composition pointed to similarities to the subseral community interpreted as *Myrico fayae-Ericetum arboreae* at El Hierro.

Moreover, certain types of current laurel forests show lower levels of disturbance, and usually represent the best-preserved areas, performing a strong argument to the creation of nature reserves. But even the characteristics of these types of vegetation might display the interference of past land use. In these cases, the areas occupied by such forests have long been abandoned or subject to less intense exploitation (Rivero *et al.* 2010). On the contrary, it is quite clear that neighboring areas with similar ecological conditions occupied by macrophanerophytic communities dominated by ericoid taxa were reflecting the impact of human land use (Arozena and Panareda 2008).

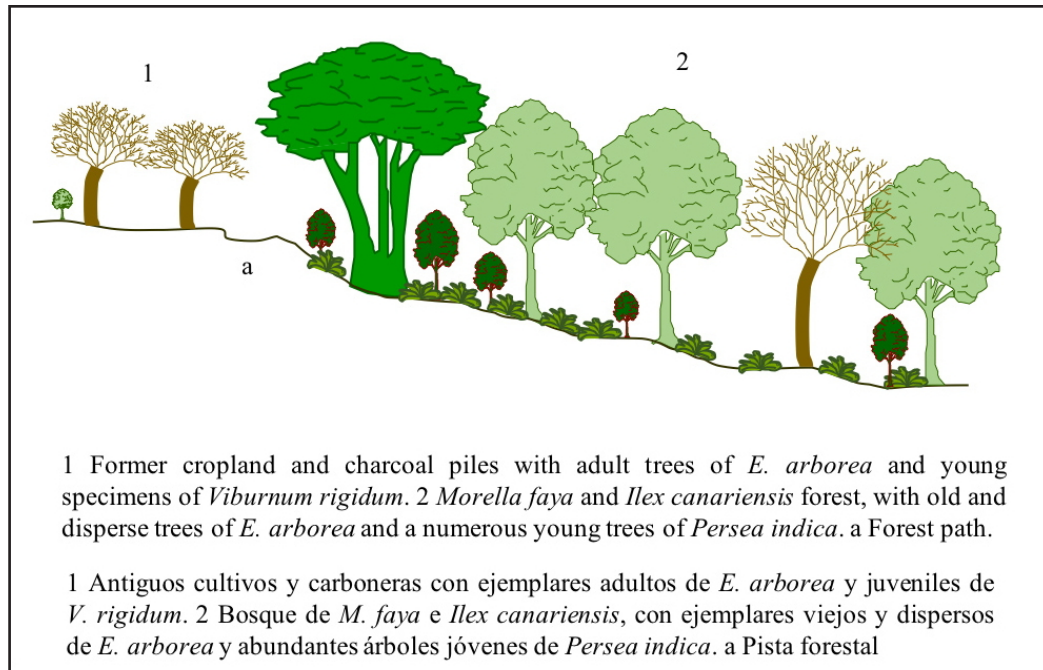
The interpretation of *Polystichio falcinelli-Ericetum arboreae* as climax (Capelo *et al.* 2004, Costa *et al.* 2012) is based on the hegemony of *E. arborea* at the tree layer, which is assumed as a sufficient floristic trait to distinguish it from the subseral community *Vaccinio padifolii-Ericetum maderinicolae*. Nonetheless, considering their attributes, these communities dominated by *E. arborea* in Madeira Natural Park must be interpreted as impoverished versions resulting from intense disturbance over centuries. This context led to the dominance of *E. arborea*, a result promoted by its ability to rapidly recover after disturbance, especially in a disturbance-resilient community dominated by such a vigorous resprouter shrub (Paula and Ojeda 2006). Moreover, this kind of floristic composition was promoted by the positive selection associated with activities such as charcoal production. Although permanent communities dominated by *E. arborea* can unquestionably develop in the poor soils found on the highest peaks of Madeira Island, it would be dubious to consider such communities as a climax stage, since their composition and structure was most likely a response to intense and long disturbance.

Interpreting such community as subseral gained more emphasis when comparing it with results from the southern sector of Garajonay National Park (La Gomera, Canary Islands), where a similar community is interpreted by Del Arco *et al.* (2006) as part of a subseral macrophanerophytic community's mosaic associated with the *Myrico fayae-Ericetum arboreae* and assumed as subseral of the *Lauro novocanariensis-Perseetum indicae*. There, the presence of old individuals of *E. arborea* with single-trunked structure, suggesting no direct exploitation, the absence of intermediate generations and the presence of herbaceous nitrophilous species (*Arenaria serpyllifolia* L and *Sonchus oleraceus* L) lead to the conclusion that some of these fo-

rest areas were used as pastures for livestock (Arozena and Panareda 2008). Although, above all, the spatial relationship among the manifestations of varying levels of maturity of the forest (figure 9) lead to the interpretation of such communities as part of a mosaic that are directly related to vegetation recovery after abandonment of agriculture, livestock and forest uses.

Furthermore, the mosaic of forest communities of the highest sector of Frontera Rural Park, structured by changes on cover of *E. arborea* and *M. faya*, is interpreted as belonging to two different phytosociological units, also with a different dynamic meaning. The forest on the windward slope is considered representative of *Myrico fayae-Ericetum arboreae* (Del Arco *et al.* 2006), and interpreted as a subseral stage associated with the degradation of the climax community *Lauro novocanariensis-Perseetum indicae*, whose suitable areas are between 800 and 1,250 m, and regularly affected by cloudbanks (Del Arco *et al.* 2006). The leeward forest, however, is considered to be a climax stage corresponding to *Pericallido murrayii-Myricetum fayae*, found in misty trade wind areas, although not influenced by them during the summer. It is located above the humid windward laurel forest (Del Arco *et al.* 2006). The subseral nature of the windward communities seems to be unquestionable, based on the relatively large presence of *E. arborea*, a characteristic heliophilous taxon. Furthermore, the multi-trunk structure of *M. faya* was the result of asexual reproduction promoted by the selective cutting of trees, while the thin trunks indicated that the exploitation of the forest occurred around 30-40 years ago.

Despite the physiognomic and cover differences of the leeward *M. faya* forest, are such attributes sufficient to interpret differently the communities of the windward side? First, multitrunked *E. arborea* were present in the canopy, although with specimens younger than those of *M. faya*. Second, all of the *M. faya* trees had a similar age and form, characterized by diverging branches that were extremely developed horizontally in their upper halves. This reveals a more or less contemporary growth when there was little competition with other species or specimens of the same taxon, allowing the horizontal projection of the canopies. These characteristics of the canopy trees are typical of recovery on areas that were deforested, nevertheless indicating the absence of a spontaneous dynamics, very likely related to positive selection of *M. faya* because of land use purposes. Third, the absence of young generations of phanerophytes further confirmed that this process was arranged by humans to obtain a "monte hueco" structure, a forest without understory that promotes optimal livestock use; it was the livestock forest structure widely diffused in the Iberian Peninsula called "dehesa". Finally, the abundance of *Urtica morifolia* (table 4, inventories 1 and 3), a species indicative of the presence of livestock, and the existence of nitrophilous *Carduus* sp., allowed deducing that until recently such forest was used as pasture for livestock.



**Figure 9.** Net contact between different forest manifestations via forest paths (Arozena *et al.* 2008).

Contacto neto entre distintos tipos de bosque a partir de pistas forestales (Arozena *et al.* 2008).

The existence of forest variants with canopy dominated by multi-trunk *E. arborea* (table 4, inventory 2; figure 8, section II), in contact with different manifestations of *M. faya* forest, suggested that forest versions found in the studied areas of Frontera Rural Park corresponded to a mosaic of the forest's reactions to different types, intensities and extent of human activities. Hence, the inheritance of the anthropic impact still masked the effect of natural factors, such as orientation and slope. Therefore, there were no enough arguments to predict with precision the attributes of the climax communities corresponding to these two forest environments.

Thus, it was difficult to accept that communities dominated by macrophanerophytic *Ericaceae* and *M. faya* in areas long disturbed by past human activities (charcoal production, timber exploitation, firewood collection, grazing, and fire) could be understood as climax communities. Collected data suggested that such communities should be interpreted as subseral.

## CONCLUSIONS

The interpretation of communities as climax is based, somehow, on a static perspective, ignoring the possibility of changes in the structure and floristic composition. Within protected areas, such interpretation might suppose specific actions to ensure conservation of those communities. This perspective might be inappropriate, since the significant reduction of disturbance by human activities

on areas assigned to protection might promote changes on communities, especially on areas disturbed by human activities along centuries.

In this paper we assume that some communities interpreted as climax are, in fact, the result of impacts from land use. From this perspective, we interpret the existence of very different floristic and physiognomic features as versions within the concept of “*fayal-breza*”, associated with disturbances of the laurel forest by human activities. Thus, it seems more advisable to interpret some communities as subseral stages, which are differentiated by the type of past land use and how long ago those uses were abandoned. This idea is based on the fact that the exploitation of forest resources in the past introduced the chance for long-term adjustments after the abandonment of such exploitation.

Concerning current features, human activity is very often a critical driving force in the configuration of the landscape, with capacity to shape the structure and floristic composition of native communities depending on land use options, even on areas where such interference is not expected. Under such perspective, current attributes must be considered transitory and not representative of climax stages. There is conviction that the type of human disturbance promotes transitory structure and composition, challenging or weakening the idea that they are climax communities. Such change might prompt adjustments in terms of environmental and territorial management approaches, without challenging major protection policies and conservation status.

Thus, instead of looking to the communities under focus as permanent, management and conservation practices should face such entities as transitory, and dedicate efforts to a better understanding of inherent dynamics. The first aim might be no longer to discern what the climax vegetation or potential of a space is, but rather to discover the processes that intervene in the current dynamics. The analysis should be focused on changes derived from abandonment: what are the most significant processes, which are the stages in the diversity of successions, what role do different environmental and anthropic factors play and how do they vary over time and space. Such perspective reveals the interference of processes and dynamics that have not been considered until now, especially on areas where impacts from land use are becoming less evident. Despite such change on perspective, protection status should never be questioned.

Furthermore, in this context, it is necessary to know if there are other factors that play a significant role on driving the attributes of vegetation communities that colonize environments that were traditionally used for cultivation or grazing. And that is a real challenge, therefore it is necessary to disentangle the real contribution of different factors, separating the effects from processes caused by global warming, or from those conditioned by socioeconomic changes. Managing a vegetation landscape that is under continuous change and satisfying the current needs of an increasingly urban society, mechanized and distant from nature, is a challenge that requires precise understanding of its dynamics and evolution, as well as a clear and lucid definition of the objectives and strategies.

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