BIOGEOGRAPHY OF AZOREAN PLANT INVADERS

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Alien plants are a major component of the Azorean vascular flora. We present a general biogeographic analysis of the taxa considered as introduced in the Archipelago. This work results from the construction of a data-base of Azorean plant invaders. Of the 996 taxa recorded for the Azores, 6,6% are considered endemic, 10,2% native, 72.6% alien, and 10,5% to be of uncertain status. The percentage of alien taxa is lowest in the Pteridophyta (26,0%) and highest in the Dicotyledoneae (78,9%). Significant differences were found between islands for the proportion of invaders. The highest percentages were found in São Miguel, Terceira and Faial, and the lowest in Flores and Corvo. A quadratic model fitted a regression between percentage of invaders and human population density, and might reflect the existence of a higher propagule pressure in some of the islands. Many of the invaders are also found in mainland Portugal and in other Macaronesian islands. The invaders are largely Palearctic in origin or Subcosmopolitan, with a wide geographic distribution, and have also been introduced in other regions of the world.

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INTRODUCTION

The study of plant invaders is important not only in academic terms, but also because some of the invaders might become noxious WEEDS (CRONK & FULLER 1995; PYSEK et al. 1995). The origin of the plants invading a certain region has been extensively covered elsewhere (DRAKE et al. 1989; GROVES & DI CASTRI 1991). Today, the success of an invader in a given ecosystem is an important indicator of whether a species might become a successful invader elsewhere (WILLIAMSON 1996).

Alien plants are a major component of the Azorean vascular flora. According to PALHINHA (1949) three quarters of the Azorean vascular plant species are exotic. Although a considerable research effort was developed regarding the native vegetation (see DIAS 1996), few papers deal with plant invaders. Exceptions are those of PALHINHA (1949, 1953), REGO (1964), SJÖGREN, (1973a, 1973b) and HANSEN (1987, 1992). Since 1992, work has been carried out on the ecology and control of plant invaders, both those originating in the Azores islands (SILVA 1994, SILVA & TAVARES 1995a, SILVA & TAVARES 1995b, SILVA et al. 1995, SILVA & TAVARES 1997, SMITH et al. 1995) and those invading the archipelago from elsewhere (SILVA et al. 1996, SILVA et al. 1997). One of the aims of this study is the development of a data-base regarding the Azorean vascular flora, including an in-depth characterisation of the introduced taxa. The Azores archipelago, located in the North Atlantic Ocean, comprises nine islands divided by three island groups (Table 1): the eastern group (Santa Maria and São Miguel), the central group (Terceira, Graciosa, São Jorge, Pico and Faial), and the western group (Flores and Corvo). The islands are of volcanic origin and the climate is temperate oceanic, with a mean annual temperature of 12°C at 550 m altitude and 17°C at 70 m, and a mean rain-fall of about 2300 and 1020 mm/year, respectively (INMG 1991).

In this paper we present a general

biogeographic analysis of the vascular plant taxa considered as introduced in the Azorean islands. We test the hypothesis that the majority of the plant invaders in the Azores have a wide biogeographic distribution.

MATERIALS AND METHODS

A data-base of the Azorean vascular flora was compiled using FileMaker Pro 2 (Claris Corporation), and based on the checklist of Macaronesian vascular plants from HANSEN & SUNDING (1993). The data-base was complemented with information regarding the included taxa, namely, from the following sources: DROUET (1866), TRELEASE (1897), PALHINHA (1966), SJÖGREN (1973b), Flora Europaea volumes 1-5 (TUTIN et al. 1964, 1968, 1972, 1976, 1980), FRANCO (1971, 1984), FRANCO & AFONSO (1994), PRESS & SHORT (1994), ANONYMOUS (1976).

Only the species stated to have been recorded as spontaneous (native or endemic - indigenous) or naturalised (introduced accidentally or intentionally by Man, but maintaining self-sustained populations) in the Azores have been included.

Searches of the data-base were carried out to ascertain how many taxa were assigned to the following categories: endemic, native, introduced, and of uncertain status. The latter category was used for taxa where it was not possible to decide if they were native or introduced. Although the reason for considering a species as introduced was largely based on records by previous authors, the following criteria, in different combinations, supported the decision to consider a species as introduced: i) first record during the last 100 years; ii) distribution limited to a reduced number of islands; iii) record of a recent extension (noted during the last 100 years) of the distribution in the Azores; iv) absence from other Macaronesian islands; v) disjunct distribution; vi) largely anthropochoric species - weeds, ornamental plants, medicinal plants. These criteria were applied after the exclusion of endemic species.
The percentage of invaders was calculated for the Pteridophyta, Gymnospermae, Monocotyledonea and Dicotyledoneae. For each of these taxa, the biogeographic distribution of the invaders was analysed. The biogeographic regions of the world used in this work are those suggested by PIELOU (1992), namely: Antarctic, Australasian, Ethiopian, Nearctic, Neotropical, Oceanian, Oriental and Palearctic. Holarctic in this text refers to the Nearctic and Palearctic regions together. Species with a wide geographic distribution, present in more than two regions were considered as Subcosmopolitan.

Percentage of invasive taxa were calculated by island. These percentages were compared using a $\chi 2$ test (ZAR 1996), followed by a multiple comparison test. For the latter analysis, percentages were transformed in degrees using arcsine after a square root transformation.

Relationships were searched for between the number of endemic, native, indigenous and exotic taxa, and the area, maximum altitude, and human population of each Azorean island. For that purpose data were log transformed, and the statistical package SPSS for Macintosh 6.1.1. was used. Linear, logarithmic and quadratic regression models were calculated, but only those indicated as significant by ANOVA were considered.

RESULTS

For the 996 taxa considered, the percentage of plant invaders in the archipelago was found to be 72,6%. The group with the lowest percentage of invaders is the Pteridophyta, while the Dicotyledoneae present the highest proportion (Table 2). About 10% of the taxa are still of uncertain status.

For every Azorean island the percentage of introduced taxa is above 50%, with a lowest proportion of exotic taxa in the western group of islands (Corvo and Flores), and the highest proportion in São Miguel, Terceira and Faial (Table 3). A relatively high proportion of native species was thus found for the western group. Species of uncertain status accounted for between 10 and 15% of the taxa.

Significant differences were found between islands for the proportion of introduced taxa ($\chi 2 = 56,94$; d.f.= 8; $p<0,0001$). Using a multiple

Table 1

Physical description of the Archipelago of the Azores.

Azorean islands	Area (km^2)	Maximum Altitude (m)	Age (MY)	Distance to mainland (km)	Human population	Density (inh./ km^2)
Santa Maria	97	587	8.120	1588	6500	66.8
São Miguel	757	1103	4.010	1584	131908	176.6
Terceira	402	1023	2.000	1764	53570	133.2
Graciosa	62	402	2.500	1844	5377	87.9
São Jorge	246	1053	0.550	1832	10361	42.2
Pico	433	2351	0.300	1860	15483	34.6
Faial	172	1043	0.730	1908	15489	89.5
Flores	142	915	2.900	2152	4352	30.7
Corvo	17	718	?	2148	370	21.6

(Adapted from BORGES 1997)

Table 2

Number and percentage of taxa from the Azorean vascular flora, divided into four categories: endemic, native, introduced, and of uncertain status.

	DISTRIBUTION OF TAXA								
Azorean	Endemic		Native		Introduced		Uncertain		Total
Vascular Flora	N	%	N	%	n	%	n	%	
Pteridophyta	9	11.7	40	51.9	20	26.0	8	10.4	77
Gymnospermae	1	20.0	1	20.0	3	60.0	0	0.0	5
Monocotyledonae	15	6.4	19	8.2	163	70.0	36	15.5	233
Dicotyledone	41	6.0	42	6.2	537	78.9	61	9.0	681
Total	66	6.6	102	10.2	723	72.6	105	10.5	996

Table 3

Distribution of the four categories of vascular plant taxa within the Azores.

	VASCULAR PLANT TAXA								
	Total	Introduced		Native		Endemic		Uncertain	
Islands		n	%	n	%	n	%	n	%
Santa Maria	435	289	66.4	66	15.2	26	6.0	54	12.4
São Miguel	730	503	68.9	91	12.5	50	6.8	86	11.8
Terceira	634	427	67.4	89	14.0	48	7.6	70	11.0
Graciosa	335	218	65.1	53	15.8	13	3.9	51	15.2
São Jorge	464	276	59.5	77	16.6	49	10.6	62	13.4
Pico	545	329	60.4	91	16.7	54	9.9	71	13.0
Faial	599	403	67.3	87	14.5	47	7.8	62	10.4
Flores	405	228	56.3	81	20.0	42	10.4	54	13.3
Corvo	305	156	51.1	68	22.3	38	12.5	43	14.1

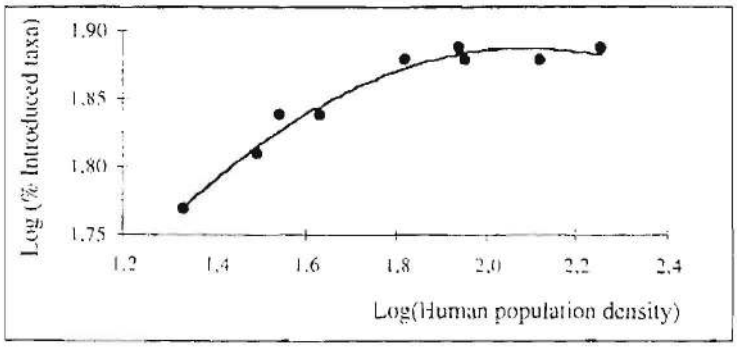

Fig.1. Relationship between human population density and percentage of introduced vascular plants in the Azorean islands. A quadratic model (R^2=0.98, F=69.2, and p=0.0001) with the following equation: log(% Introduced taxa) = $-0,18\ \log(\text{Density})^2 + 0.75\ \log(\text{Density}) + 1.09$.

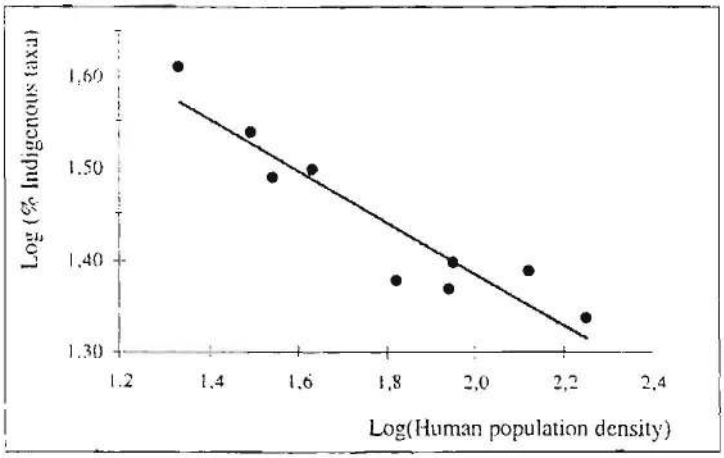

Fig. 2. Relationship between human population density and percentage of indigenous vascular plants in the Azorean islands. A linear model (R^2=0.88, F=51.6 and p=0.0002) with the following equation: log(% Indigenous taxa) = -0.28 log(Density) + 1,94.

comparison test significant differences were found between São Miguel and the islands of the western group (Table 4). No significant differences were found between Corvo, Flores, São Jorge and Pico, but all the remaining islands presented a proportion of invaders significantly different from that of Corvo.

A quadratic relationship was found between human population density and the percentage of introduced species (Fig. 1). A linear model was adjusted to the relationship between human population density and the percentage of indigenous species (Fig. 2).

A considerable proportion of the introduced plants found in the Azores was also present in mainland Portugal and in other Macaronesian islands (Table 5). The Pteridophyta were an exception, with only a quarter of the introduced taxa found in mainland Portugal.

A large proportion of the introduced Pteridophyta have a Subcosmopolitan or a Palearctic distribution or are present in more than one biogeographic region (Fig. 3). The Gymnospermae has only three naturalised species: one taxa from America, one from the Mediterranean, and a third from Asia. The Monocotyledoneae also present a large proportion of Palearctic and Subcosmopolitan taxa (Fig. 4). The same was found for the Dicotyledoneae, although this group also presents a considerable

Table 4

Percentage of introduced vascular plants in the Azores arquipelago. The percentages were re-calculated after excluding species of uncertain status. Comparison between islands ($\chi 2$ test.followed by a multiple comparison test).

Azorean Islands	Percentage of plant invaders	Comparison α=0.05		
Corvo	59.5	a		
Flores	65.0	a	b	
São Jorge	68.7	a	b	c
Pico	69.4	a	b	c
Faial	75.0		b	c
Terceira	75.7		b	c
Santa Maria	75.9		b	c
Graciosa	76.8		b	c
São Miguel	78.1			c

(Different letters = significant differences.)

proportion of introduced taxa occurring in two biogeographic regions, and some exclusively Macaronesian taxa (Fig. 5).

DISCUSSION

The percentage of invaders found in the Azores is higher than that found in other places of the world (REJMÁNEK et. al. 1991, MONTENEGRO et al. 1991, WELLS, 1991), even when compared with islands presenting a very much modified vegetation such as Hawaii and New Zealand, with 17,5-19% and 47% of introduced species, respectively (HEYWOOD 1989). Some authors suggest that isolated oceanic islands are predisposed to certain types of human-related invasions (LOOPE & MUELLER-DOMBOIS 1989), others (WILLIAMSON 1996) consider that this has yet to be proved. The Azores are considerably remote islands, and are relatively young when compared with the other Macaronesian archipelagos. They have been intensively cultivated since the XV century. Many species have been introduced for food and fibre or as accompanying weeds, and also as ornamental and hedging plants. A large proportion of the landscape was directly changed by human activities, allowing the easy entrance of exotic species, and increasing the propagule pressure, the amount and frequency of introduction of dispersal units from an alien species.

The islands of the western group, together with São Jorge and Pico, are those presenting a lower proportion of invaders. We might thus suggest that they were under a relatively lower propagule pressure. A lower human population density allowed a lower input of alien species. São Miguel, Terceira and Faial are more heavily populated islands and also present the higher proportions of alien taxa. Furthermore, these islands have been considered as an important source of propagules from alien taxa for the other islands, during the last one hundred years (SJÖGREN 1973a). Graciosa and Santa Maria are small islands with a relatively low maximum altitude where the landscape was largely altered by human action. This might have lead to a relatively high input of alien taxa, what might explain the relatively high proportion of invaders recorded for these islands.

Differences between islands for the proportion of introduced taxa, might thus be associated with different levels of human pressure on the

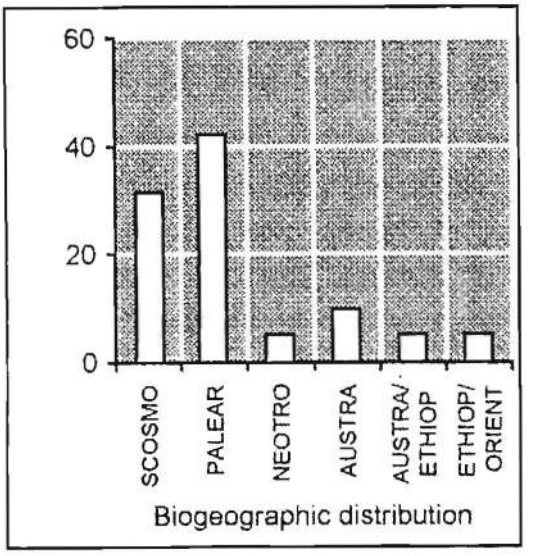

Fig. 3. Biogeographic distribution of Pteridophyta introduced to the Azores: total of 20 taxa.

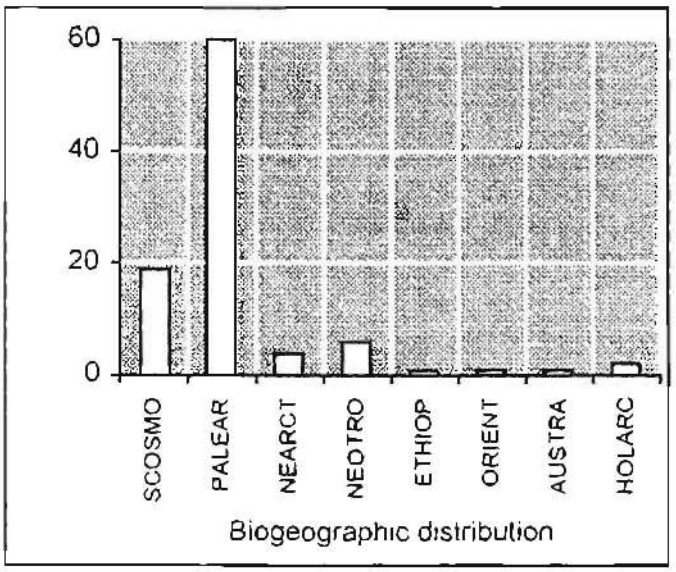

Fig. 4. Biogeographic distribution of Monocotyledoneae introduced to the Azores: total of 163 taxa.

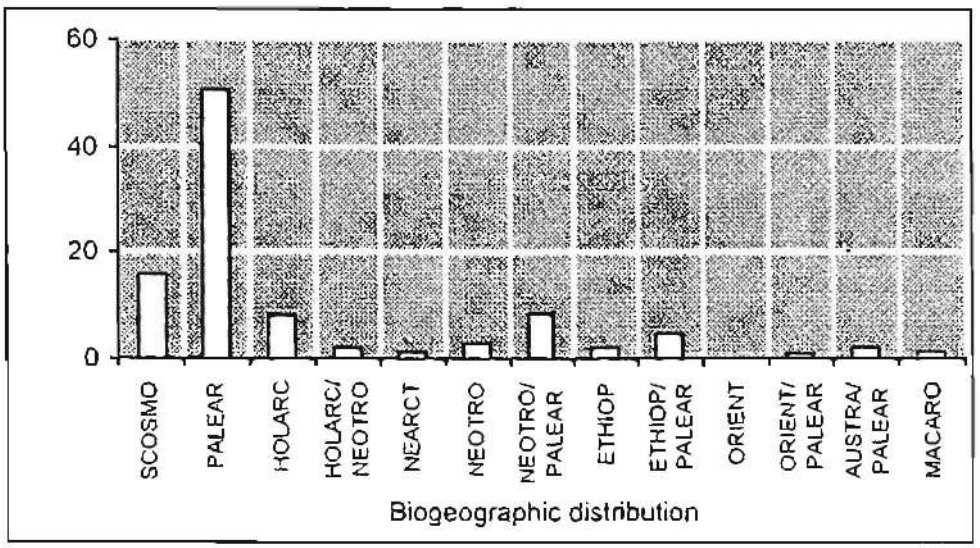

Fig. 5. Biogeographic distribution of Dicotyledoneae introduced to the Azores: total of 537 considered taxa.

environment, implying different levels of propagule pressure. The models derived from our analyses positively relating the human population density to the percentage of introduced species further support this hypothesis. WILLIAMSON (1996) reports studies where similar results were found when relating numbers of plant invaders and numbers of human visitors into nature reserves, higher numbers of visitors were associated with a higher proportion of invaders. Quarantine measures should be implemented to to avoid further introductions in the less affected islands.

A considerable proportion of Azorean plant invaders is also present in mainland Portugal or in other Macaronesian islands, what might suggest a

Table 5

Percentage of introduced taxa from the Azorean vascular flora which also occur in three regions outside Azores: mainland Portugal, Madeira island and the Macaronesia excluding the Azores. (n=number of introduced taxa)

INTRODUCED		% OF TAXA		
VASCULAR PLANTS	n	Portugal	Madeira	Macacaronesia
Pteridophyta	20	25.0	55.0	60.0
Gymnospermae	3	66.7	33.3	33.3
Monocotyledonae	163	70.6	63.2	71.2
Dicotiledonae	537	77.8	67.2	75.2

direct introduction of plants from the mainland, but also that many of those species are successful invaders elsewhere. Success as an invader in other ecosystems should be used in the future to reject a potential introduction, and also to stimulate the control of species that were already introduced but still with a limited distribution.

Many of the invaders have a Subcosmopolitan distribution, are present in two biogeographic regions or have a Palearctic distribution, i.e. always a wide distribution. This further emphasises the suggestion that success as an invader in other regions is a good indicator of the potential for similar success in the Azores. Thus, we might conclude that, as a general rule, the potentially most successful invaders in the Azores are those species with a wide biogeographic distribution which are already invaders elsewhere.

Some of the invaders present a very narrow biogeographic distribution, for example *Clethra arborea* Aiton (Clethraceae, endemic to Madeira but an invader in São Miguel), and do not followthe general scheme.

Also, some of the invaders are considered as weeds in agriculture, forestry and in nature reserves, for example *Rumex* spp. (Polygonaceae) and *Mentha suaveolens* Ehrh. (Lamiaceae) on pastureland, *Hedychium gardnerianum* Ker-Gawl (Zingiberaceae) in forestry and in nature reserves, and *Pittosporum undulatum* Vent. (Pittosporaceae) from sea level up to 600 m. Both groups deserve further study regarding their ecology and control.

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