Native or introduced? Fossil pollen and spores may say. An example from the Azores Islands

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Summary

Aim: Among the various possible approaches to assess whether a species is native or introduced, the analysis of subfossil pollen and spores from natural archives is a valuable tool. Requirements include a sufficiently high taxonomic resolution of the pollen morphology, as well as sufficient temporal and spatial resolution. The aim of this study is to show the usefulness of this method in solving whether the taxon is native or introduced.

Location: The results are derived from two islands of the Azores: Flores and Pico.

Methods: Analysis of pollen and spores in lake sediments; radiocarbon dating of the studied sediments.

Results: *Selaginella kraussiana* (Kunze) A. Braun has occurred on the Azores Islands at least for the last 6000 years.

Main conclusions: Different authors had assigned three different types of status to *Selaginella kraussiana*: native, introduced (invasive), or uncertain. High numbers of spores of this taxon were present in the sediment cores from the two studied lakes already several thousand years before the Portuguese discovery and the Flemish settlement in the 15th century. This proves that the species is native on the Azores Islands. Pollen and spore analysis can therefore contribute to historical biogeography not only regarding questions about pre-Quaternary plate tectonics but also about early human impact.

Key words: palynology, Holocene, *Selaginella kraussiana*.

1. Introduction

Invading species are an increasing threat to many native floras and faunas (Williamson 1996; http://www7.nationalacademies.org/usnc-diversitas/index.html), and small isolated areas such as oceanic islands seem to be especially vulnerable. The causes for the increasing threat may primarily come from increasing propagule pressures due to human impacts, such as trans-continental travel and transport (either by ship or plane), but also global warming may play a role, because it may shift the climatic constraints of species.

The causes of the high vulnerability of island floras and faunas are often discussed in the vast field of Island Biogeography, in which data collection and hypothesis generation interact in a fascinating way (e.g. Vitousek et al. 1995; Whittaker 1995, 1998). Six conditions (Cronk & Fuller 1995) may explain why oceanic islands may be especially susceptible to invasions ("oceanic" here means mid-ocean, as opposed to continental shelf):

1) species poverty (because of great distances from continents),
2) evolution in isolation,
3) early European colonisation,
4) small spatial scales,
5) crossroads of international trade, and
6) ecological release (alien species may arrive without natural pests).

To collect reliable data on invasions, the first step is to clarify which species are native and which are not, and if not, when were they introduced. The most important criteria were listed by Webb (1985): fossil evidence, historical evidence, habitat, geographical distribution, ease of naturalisation elsewhere, genetic diversity, reproductive pattern, and supposed means of introduction. These criteria were used by one of us in an attempt to analyse the flora of the Azores (Schäfer 2003). An approach combining phytosociological, ecological, phytogeographical, and historical data was recently presented by Decocq et al. (2004). The use of fossil pollen to answer status questions has been criticised because the taxa are usually identifiable only to genus level, and doubts about long-range transport remain (Webb 1985).

Here we show that under certain conditions pollen and spores in lake sediments can be very useful to clarify status problems. As an example we discuss the species *Selaginella kraussiana* (Kunze) A. Braun on the oceanic Azores archipelago, to which different authors assigned three different types of status: native, introduced (invasive), or uncertain (see Table 1). Palynology in lake sediments provides a datable record of its spores. Presence or absence of the plant before the first discovery and settlement of the Azores in the late 15th century can thus be assessed.

2. Material and methods

2.1 Taxonomic and biogeographical background

Selaginella kraussiana (Selaginellaceae) is a heterosporous pteridophyte related to the clubmosses and has characteristic reticulate, narrowly winged megaspores (c. 750 μm) and echinate microspores (26-32 μm) with bases of spines joined to form ridges. It was described as *Lycopodium kraussianum* by the German botanist G. Kunze in 1844 on the basis of a specimen collected by C. von Krauss 1839 in Natal, South Africa (Kunze 1844). It was later transferred to the genus *Selaginella* (Braun 1860) and reported as native throughout the African continent from the Cape to Sudan and Ethiopia, and from Sierra Leone to Kenya and Mozambique (e.g. Hassler & Swale 2002). It is widely planted as an ornamental, certainly the most common *Selaginella* in cultivation worldwide, and it has been reported as an escaped, naturalised, or invasive species from the Neotropics (Brazil, Panama, Jamaica, Hawai'i), the southern USA (California, Alabama, Georgia, the Carolinas), South Australia, New Zealand, and several W-European countries (Portugal, Spain, Great Britain, France, Belgium) (e.g. Wilson 1996). It is common on the Canaries, Madeira, and all islands of the Azores (Schäfer 2003) but its status in the middle-Atlantic islands is controversial (see Tab. 1). It cannot be a Tertiary relict because the Azorean islands are too young: the oldest rocks are c. 5 million years old (Féraud et al. 1980).

2.2 Palaeoecology

We studied sites on two different islands of the Azores. Flores is the westernmost island, and like all Azorean islands of volcanic origin. It is situated on the Ameri-

Table 1: Taxonomy and biogeography of *Selaginella kraussiana* and *S. azorica.*

Literature	*Selaginella kraussiana* (G. Kunze) A. Braun	*S. azorica* Baker
Seubert & Hochstetter 1843; Watson 1844; Seubert 1844	**Native** (as *Lycopodium denticulatum*)	–
Drouet 1866	**Native** (as *Selaginella denticulata*)	–
Watson 1870	**Native;** this species has always passed (..) for *Lycopodium (Selaginella) denticulatum* (..) Those reserved for my herbarium belong to *Kraussiana* (..) I assume this to be equally true also of the *Selaginella* recorded as *denticulata* in the works by Seubert and Drouet.	–
Baker 1883 & 1884	Cape Colony, Natal, Fernando Po, Cameroon Mountains, **Azores**, Madeira, and reported also from Sicily. '*S. Brownii* Hort. Stansfield' is a dwarf variety from the Azores.	**Described as new endemic of the Azores** (based on single, sterile specimen collected by Arruda Furtado in the "mountains of the Azores")
Trelease 1897	**Native, common**	**Endemic to the Azores, rare or local** (not seen)
Gandoger 1899	**Endemic (or almost endemic) to the Azores**	**Endemic (or almost endemic)** to the Azores
Tutin & Warburg 1932	Not mentioned	**Endemic to the Azores** (Faial, Pico)
Palhinha 1943	**Native**; Azorean and African specimens identical	**Endemic to the Azores** (not seen)
Dansereau 1961	**Macaronesian-African**	**Endemic to the Azores** (not seen)
Palhinha 1966	**Subspontaneous**, native in tropical and S Africa; commonly cultivated in continental Portugal	Synonymous to *S. kraussiana*
Ward 1970	**Native**; ubiquitous as extensive mats in woods, fields, and calderas	Synonymous to *S. kraussiana*? more work is needed
Franco 1971	**Introduced to the Azores** and to Portugal, native in tropical and South Africa	Not mentioned
Sjögren 1973	Now frequent in most plant communities on all islands; probably extension of the distribution during the last 100 years	Not mentioned
Nogueira 1980	Spores or fragments of this species could have been brought to the Azores together with seeds or ornamental plants imported from S Africa, ... **Today it is perfectly adapted, ... and almost showing characters of native status.**	Synonymous to *S. kraussiana*
Dostal 1984	**Native on the Azores** (and Central and Southern Africa), in gardens since 1800, often escaped and found in Belgium and Northern Italy	Synonymous to *S. kraussiana*
Valentine & Moore 1993	Native in tropical and southern Africa. **On the Azores status doubtful, possibly native**, in some western European countries not native	Synonymous to *S. kraussiana*
Schäfer 2003	**Escaped** ornamental plant, **naturalised** and invasive; native to tropical and S Africa	Synonymous to *S. kraussiana*

can continental plate. The island was probably discovered in the early 14th century (Bento 1993) but remained uninhabited until 1472 when Wilhelm van der Haegen founded a small settlement near the coast (Frutuoso 1589). Its landscape contains seven crater lakes. Lagoa Rasa on Flores (39° 24.49823' N, 31° 13.49822' W, 530 m a.s.l.) is, as the name suggests, a shallow lake. In 1998 we obtained 340 cm of sediment beneath 620 cm of water with a square-rod piston corer (Wright 1991). Radiocarbon dates on terrestrial plant macrofossils were obtained at Utrecht and Poznan (details follow in Amman et al. in prep.). For the pollen analysis of 45 samples reference material from the Palynological Laboratory of the Instituto Português de Arqueologia (Lisbon) was used as well as the keys of Reille (1992) and Punt & Blackmore (1991).

Further palynological information comes from Lagoa da Caveiro on the island of Pico (38° 26.10' N, 28° 11.79' W, 903 m a.s.l.), whose volcano is the highest mountain of Portugal, situated on the Eurasian plate in the central group of the Azores. The 625 cm of sediment, mainly clay gyttja and gyttja, has a robust chronology based on >20 radiocarbon dates.

3.Results

The sediment of Lagoa Rasa on Flores is mainly organic gyttja, and the lowermost 1.5 cm is compressed. Volcanic material, e.g. pyroclastics, were not reached. The depth-age relationship is based on five radiocarbon dates.

The complete results of pollen analysis of Lagoa Rasa will be discussed in a separate paper focussing on the composition of the vegetation before and after human impact (Ammann et al. in prep.). In Fig. 1 we present a summary diagram and the record of *Selaginella kraussiana.*

The taxon in question, *Selaginella kraussiana,* shows high values since the beginning of the record, about 2435 radiocarbon years BP, i.e. about 500 BC (calibrated). The record of this very characteristic microspore is continuous throughout the approximately 2500 years recorded, whereas human impact sets in during the late 15th or early 16th century AD (at about 190 cm sediment depth).

Spores of *Selaginella kraussiana* were also encountered in the sediments of Lagoa do Caveiro on Pico (analysis: T. Rittenour). This lake has so-far the longest sediment record found on the Azores, and the oldest cored sediments are radiocarbon dated to ca. 4000 years BC (calibrated). High values of *Selaginella kraussiana* spores (up to 27 %) were found in the oldest sediments and throughout the sediment sequence.

These finds show that the taxon is native to at least two islands of the Azores archipelago, Flores and Pico.

4. Dicussion

Pielou (1992) states: “Oceanic islands (..) can only have acquired their biota by jump dispersal”, and “waif biota (..) are disharmonic – they contain a disproportionately high number of organisms adapted to jump dispersal.”

Selaginella kraussiana on the Azores receives three different biogeographical statuses, i.e. native, introduced/escaped/naturalised/invasive, or uncertain and was even listed as Azorean endemic by Gandoger (Tab. 1). It was first collected on the Azores by C. F. Hochstetter in 1838 and considered as a native species but confused with *Selaginella denticulata,* which had never been collected in the Azores. In 1870 H. C. Watson in his revision of the flora of the Azores identified the Azorean specimens as *S. kraussiana*

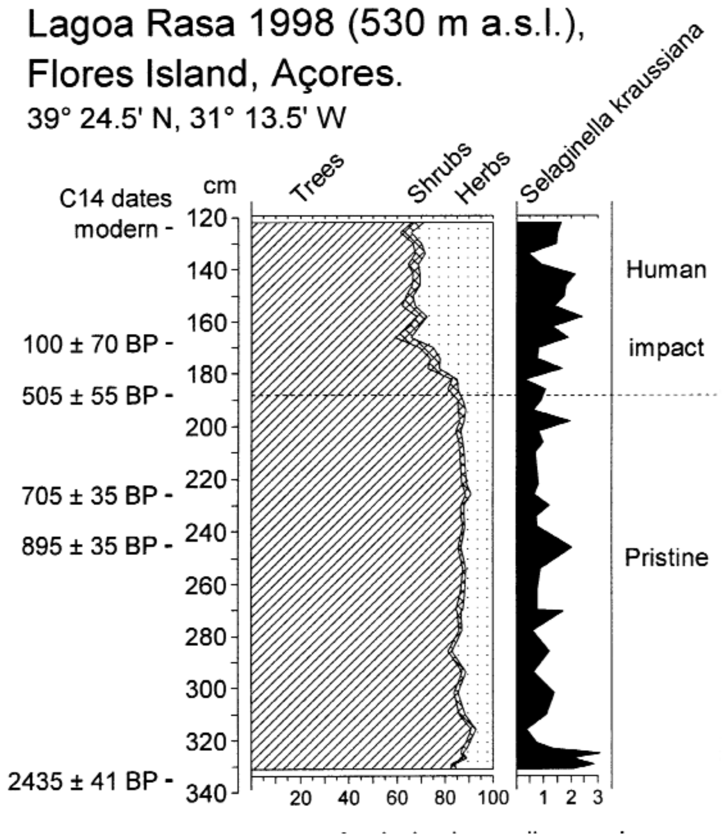

Fig. 1: Pollen and spore percentages.

(Watson 1870). Baker (1883) described a new endemic *Selaginella azorica* on the basis of a single, sterile specimen collected by Arruda Furtado in the Azores. This taxon was cited as Azorean endemic by several authors (Tab. 1), but it was actually seen on the islands (on Faial & Pico) only by Tutin & Warburg (1932), who do not mention *S. kraussiana*, which today is a very common plant on both islands. Alston (1956) stated that the type of *S. azorica* is in fact only a form of the variable *S. kraussiana,* which is the only *Selaginella* reported from the Azores within the past 40 years. Thus we conclude that the taxonomic questions have been clarified and therefore concentrate on the question of the biogeographical status of *S. kraussiana* on the Azores.

The degree of **dispersibility** of propagules is a major factor for the colonisation of oceanic islands. Spores and minute seeds can be transported very easily by wind. Adsersen (1995) in his overview of groups of organisms and their dispersibility mentions spores as the smallest entities and therefore with the lowest percentage of endemism. This is certainly true for bryophytes with many cosmopolitan species. However, there seems to be a considerable difference in dispersibility between bryophyte and pteridophyte spores. Among the bryophytes of the Azores very few true endemics occur, but among the c. 66 endemic vascular plant species of the Azores are seven pteridophytes (Schäfer 2003). Apparently these pteridophytes were unable to reach the nearby Madeira group, where they could have established populations under similar ecological conditions. In the opposite direction, other pteridophytes such as *Selaginella denticulata* (not rare on Madeira), never seem to have reached the Azores. The transport of short-lived spores of certain ferns that depend on high humidity and of large *Selaginella* megaspores, which are produced in comparatively small numbers, seem to be much more difficult than the transport of small bryophyte spores. Thus, the first megaspores of *Selaginella kraussiana*, which has the largest megaspores of its genus, were probably not transported by wind directly from the African continent to the Azores but originated from populations established earlier on Madeira. The total distance that had to be covered by wind transport is then reduced to c. 800 km.

Sauer (1988) suggests that spores follow "Beijerinck's Law: everything is everywhere but the environment selects". This would imply that the microspores of *Selaginella kraussiana* observed in the presettlement sediments might have resulted from long-distance transport from the African population, and it would then not indicate the local presence of the plant on the islands of Flores and Pico. But we feel confident that we can exclude long-distance transport here for most of the microspores for the following reasons: (1) the spores are present in every sample studied, (2) the spores reach quite high percentages (ca. 2.5 % in Lagoa Rasa and >25 % in Lake Caveiro), and (3) high percentages are reached in a period with rich communities, including high pollen- and spore-producers, so the high spore percentages are not a result of generally low pollen or spore production.

Historical biogeography, as the interface between biogeography and geology, usually attempts to explain disjunct range patterns with either plate tectonics or Pleistocene glaciations as potential causes. But for the question of native or introduced, shorter time scales and a higher temporal resolution are required. Human impacts on flora and fauna are a phenomenon of the Holocene, i.e. the last 11,500 years, in which a temporal resolution of 50 years or less is appropriate. On many remote islands, like the Azores, the time period of human impact can be reduced to only a few hundred years.

The precondition for the assessment of a native or introduced status of a species is that the taxon produces sufficient and identifiable fossils (such as pollen, fruits, chitinous remains). The fossils should therefore be morphologically unique, and the animal or plant should have lived close enough to the basin where the fossil is archived (usually a lake or mire). Organisms that are not recorded are those without hard fossilising parts (e.g., many amoebae), groups producing fossils that cannot be identified to species or genus level (e.g., pollen of Poaceae), and species producing good fossils but in insufficient numbers (e.g., entomophilous plants of a dry meadow). In the middle-Atlantic islands, the absence of adequate lakes or peat bogs is also a major problem (e.g., Canaries, Madeira, Cabo Verde, lowland regions of the Azores). But even with this restriction, palaeoecology and biostratigraphy of Holocene deposits can clarify at least some cases of unclear status.

Conclusions

With palaeobotanical methods we could unequivocally confirm the status of *Selaginella kraussiana* as native on the Azores islands. Its populations on

Madeira and the Canary Islands are probably also native and can be considered as the connecting link between the main African populations of *Selaginella kraussiana* and the remote Azores populations.

For certain groups of organisms high-resolution studies in Holocene lake sediments and peats may answer the question when a certain taxon arrived in the area. The time of its arrival can then be compared to the traces of prehistoric or historic human impact on the vegetation and environment. This may give a clue whether the taxon is native or introduced. For plants, the analysis of pollen, spores, and macrofossils may provide an answer. Thus we may fulfil the promise of "A Factual Basis for Phytogeography" expressed by the subtitle of Sir Harry Godwin's (1975) monumental work "The History of the British Flora". We may thus contribute to "historical biogeography" by concentrating on the Holocene and on human impact, thereby providing an interface between palaeoecology, biogeography, and our efforts to recognise early invasions.

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