

When is an invasive not an invasive? Macrofossil evidence of doubtful native plant species in the Galápagos Islands

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Abstract. The Galápagos Islands are globally renowned for their ecological value and as a world symbol of scientific discovery; however the native biodiversity of this unique region is currently under threat. One of the primary concerns is the detrimental impact of approximately 750 nonnative plants introduced over the last 500 years of human presence in the archipelago. In addition to these known introduced species, there are an additional 62 vascular plants classified as “doubtful natives,” where native status remains unclear. To help address the questions of provenance regarding these doubtfully native species and their impact on highland ecosystems over the past 500–1000 years, we analyzed plant macrofossils in sedimentary records. Appropriate species classification (native or introduced) was determined using baseline data of species presence on the islands. We confirmed that six plants (*Ageratum conyzoides*, *Solanum americanum*, *Ranunculus flagelliformis*, *Brickellia diffusa*, *Galium canescens*, and *Antheophora hermaphrodita*) once considered doubtful natives or introduced are actually native to the Galápagos flora. These results have relevance not just for the Galápagos but also many other oceanic islands in demonstrating the application of palaeobotanical data to conserving and restoring native biodiversity.

Key words: conservation management; doubtful natives; Galápagos Islands; introduced species; macrofossils; species provenance.

INTRODUCTION

Island ecosystems worldwide have been subjected to biological invasions following the settlement of humans, widely recognized as one of the greatest threats to biodiversity. Unfortunately the Galápagos Islands, despite their relatively late human occupation (human presence did not begin until European discovery in AD 1535 [Froyd et al. 2010]) and unusually high native species retention with ~95% of terrestrial biodiversity remaining intact (Tye et al. 2002), still face significant threat from invasive species (Magee et al. 2001). Recent plant introductions are estimated to be over 13 000 times the historic natural species arrival/establishment rate (Tye 2006). Today, the pressures placed by humans upon the Galápagos are dramatically transforming ecosystems particularly in the humid highlands of the larger more developed islands, where approximately 88% of the habitat on the island of Santa Cruz and 94% on San Cristobal are now classed as transformed (Watson et al. 2009).

It is known worldwide that prior to the 1800s Europeans settling in newly discovered lands caused both widespread introductions (intentional and unintentional) of nonnative species and rapid extinctions of local flora and fauna; however, the harsh conditions in the Galápagos allowed the islands to largely escape this early colonization influence. More recent introductions, however, either intentionally for agricultural, horticultural, or medicinal purposes, or unintentionally introduced through external sources (e.g., increased travel to the Islands) has led to an estimated 750 introduced plants present in the archipelago today (Guézou et al. 2010). In addition to these known introductions are 62 species classified as doubtfully native, species for which it is unknown whether they are introduced or native to the Galápagos (Tye et al. 2002). Definitive determination of the provenance of these species will aid conservationists in understanding the extent and impact of nonnative species in the Galápagos highlands and in the design of effective ecological restoration programs.

The objective of this study was to provide a scientifically robust record of the occurrence of some of these doubtfully native plant species in the Galápagos Islands utilizing the taxonomic precision of macrofossil identification, and to examine their variation in abundance, both before and after human settlement. This

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work supplements previous palynological investigations by van Leeuwen et al. (2008). The aims of the analysis were two-fold. First, to determine the timing of arrival of doubtful natives; did they first occur in the fossil record before human presence in Galápagos, providing evidence of their native status, or does their appearance in the fossil record coincide with a specific anthropogenic activity, e.g., onset of agricultural activity/grazing on the islands? Second, to reconstruct the natural variability and abundance of the doubtful natives through time; in some studies elsewhere, for example, it has been demonstrated that whilst some 'invasive' plants are in fact native, i.e., they have a fossil record that predates human impact, their abundance has increased greatly with the onset of agriculture in the region and therefore their increased abundance is as a result of human impact (Lynch and Saltonstall 2002).

METHODS

Study site

The sediment of two *Sphagnum* bogs, referred to as East Bog (0°38'45" S, 90°19'03" W, 739 m elevation) and Psidium Bog (0°38'38" S, 90°19'37" W, 809 m elevation), was examined from the island of Santa Cruz, a large central island in the Galápagos archipelago located approximately 960 km west of mainland Ecuador (Appendices A and B). Both bogs are situated in cinder cone craters located 1.2 miles (1 mile = 1.61 km) apart on the southern slope of the Cerro Crocker ridge. No perennial streams flow into the craters providing closed basin systems with steep, vegetated banks for input of macrofossils. The moisture to maintain the *Sphagnum* bogs comes from heavy precipitation and/or semipermanent mist, termed garúa. The landscape surrounding the bogs is dominated by the native high elevation fern-sedge communities of the Humid vegetation zone (Tye and Francisco-Ortega, *in press*). The vegetation directly surrounding the bogs within the craters themselves is composed of an herb and fern layer, including *Cyathea weatherbyana*, *Pteridium aquilinum* var. *arachnoideum*, *Ageratum conyzoides*, and *Cyperus grandifolius*. The bog surfaces are covered with a thick mat of *Sphagnum* spp., *Gleichenia* spp., *Blechnum* spp., *Pernettya howellii*, *Azolla microphylla*, *Lycopodium clavatum*, and *Lycopodium cernuum*.

Sediment analysis

Sediment cores were obtained using a modified Livingstone Piston Sampler Wright et al. 1984). Consecutive 1-m segments (East bog, 280 cm final length; Psidium bog, 235 cm final length) were extracted in the field, wrapped in plastic film and aluminum foil, encased in hard plastic tubes and stored at 4°C at the Long-term Ecology Laboratory, Oxford, UK.

Sediment lithology was described using the Troels-Smith method (Troels-Smith 1955; Appendix C). Sediment samples (50 cm³) were taken at 8-cm intervals for macrofossil analysis, following the protocol de-

scribed in Birks (2001). The total number of macrofossil seeds, seed fragments and plant parts > 125 µm for each sample (up to 1000 per species) was tallied using a Nikon SMZ800 stereo-microscope (Nikon Instruments, Melville, New York, USA). Detailed taxonomic examination was performed using an Olympus BX40 high-power light microscope (up to 100× magnification; Olympus America, Center Valley, Pennsylvania, USA) as well as a scanning electron microscope (SEM). The fossil samples were identified using seed/plant identification guides (Delorit 1970, Wiggins and Porter 1971), and a reference collection of over 500 vascular plant species developed by the authors from both modern-day plant material in the Galápagos and herbarium samples from the Charles Darwin Research Station (CDRS). Samples were also compared to the herbarium collection in the Missouri Botanical Garden (MBG). Between 15 and 20 seeds from each resource (CDRS and MBG herbarium samples) were examined using SEM imagery to confirm the species identification. Due to the highly unique surface structure and individualized shape of seeds identification between species can be determined. Results were analyzed and displayed using TILIA, TILIA GRAPH (Grimm 1990), and Psimpoll software programs (the Psimpoll software is *available online*).⁶

Dating

Eight organic peat and gyttja sediment samples from the *Sphagnum* bogs were dated to determine the age of the core sequences, using both AMS (accelerator mass spectrometry) and conventional (gas proportional counting) dating (Appendix D). All dates were calibrated to calendar years before present (cal yr BP) using the Southern Hemisphere terrestrial calibration curve SHCal04 (McCormac et al. 2004) in Oxcal 4.0 (Bronk Ramsey 2001). Cubic spline (East Bog) and linear (Psidium Bog) age-depth models were used to interpolate age of the sequences between ¹⁴C dated sections of each core.

RESULTS

Lithological analyses reveal that both sites likely contained open bodies of water before transitioning to *Sphagnum* peat approximately 685 years (East Bog) and 470 years ago (Psidium Bog; Appendix D). The East Bog sequence was shown to span the last 5000 ± 100 cal yr BP years (Appendix D). Of the 76 different plant macrofossil types discovered at the site (E. E. D. Coffey, C. A. Froyd, and K. J. Willis, *unpublished data*), five were identified as doubtful natives (Fig. 1): *Ageratum conyzoides*, *Antheophora hermaphrodita*, *Galium canescens*, *Ranunculus flagelliformis*, and *Solanum americanum*.

Seeds and seed fragments of *Ageratum conyzoides* and *Galium canescens* are abundant throughout the record,

⁶ (<http://www.chrono.qub.ac.uk/psimpoll/psimpoll.html>)

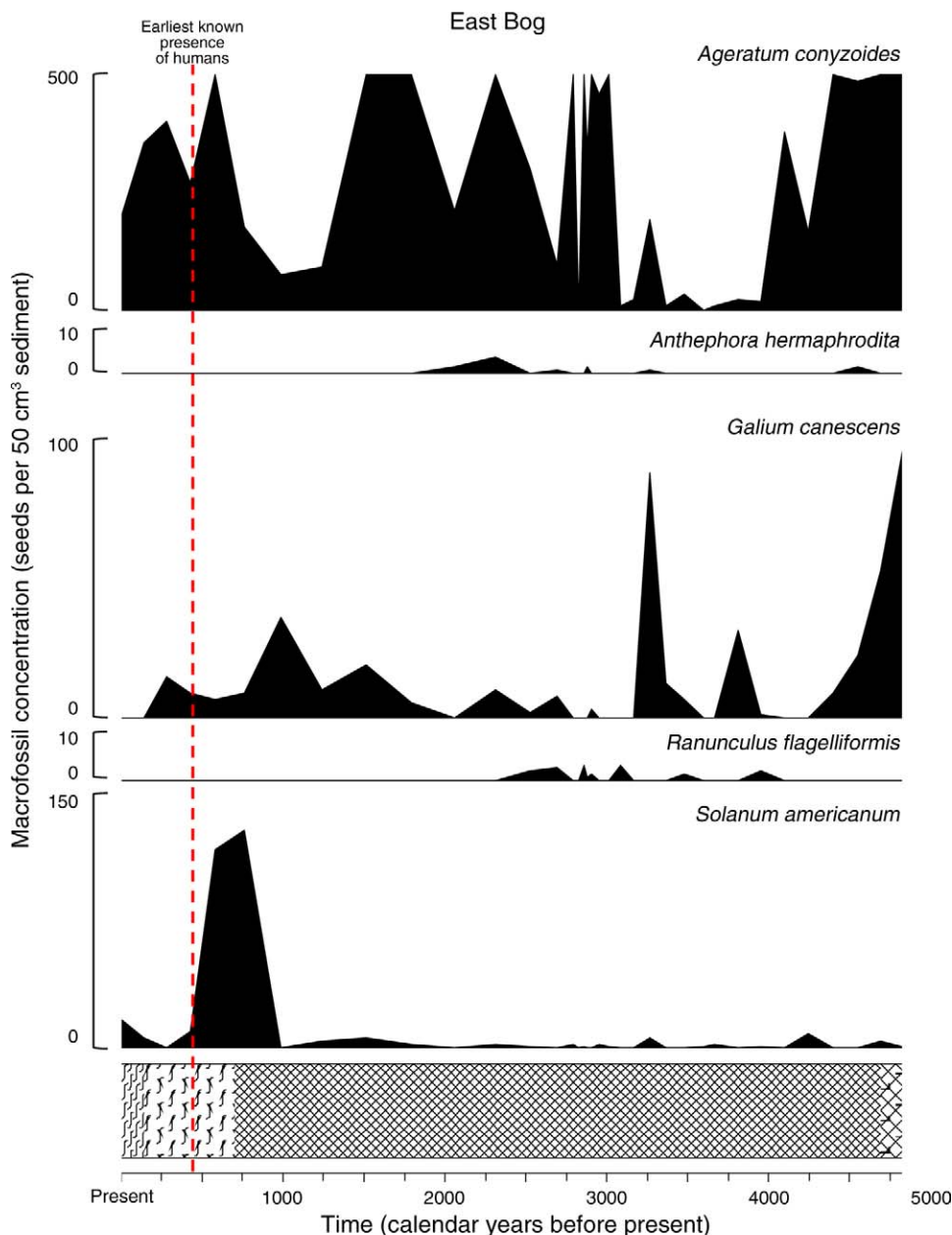


FIG. 1. Macrofossil results for doubtful native species from East bog in the Santa Cruz highlands, Galápagos Islands: concentration diagram of seed fragments $>125 \mu\text{m}$ in 50 cm^3 of sediment. Radiocarbon dates are calibrated calendar year before present (BP). The red dashed line indicates the earliest known presence of humans in the archipelago as a whole.

from 5000 ± 100 cal yr BP (mean \pm SD) to the present, although both exhibit variability. There is a decline in *A. conyzoides* during $\sim 4000\text{--}3100 \pm 100$ cal yr BP, after which it recovers and continues to the present. *G. canescens* seeds are most plentiful early in the record during $5000\text{--}3350 \pm 100$ cal yr BP. Both *Ranunculus flagelliformis* and *Anthephora hermaphrodita* occur throughout the core in moderate numbers. *A. hermaphrodita* is found as early as $\sim 4550 \pm 100$ cal yr BP although occurrence is sporadic, with the largest

abundance at 2300 ± 100 cal yr BP. The first occurrence of *R. flagelliformis* is around 4800 ± 100 cal yr BP and remains in small abundance until 2500 ± 100 cal yr BP. Although not present in the recent macrofossil record, both *A. hermaphrodita* and *R. flagelliformis* occur in the Santa Cruz highlands today. The earliest evidence of *Solanum americanum* is at approximately 4700 ± 100 cal yr BP, remaining in very low numbers until a large increase occurs during $\sim 970\text{--}445 \pm 50$ cal yr BP (AD 980–1505).

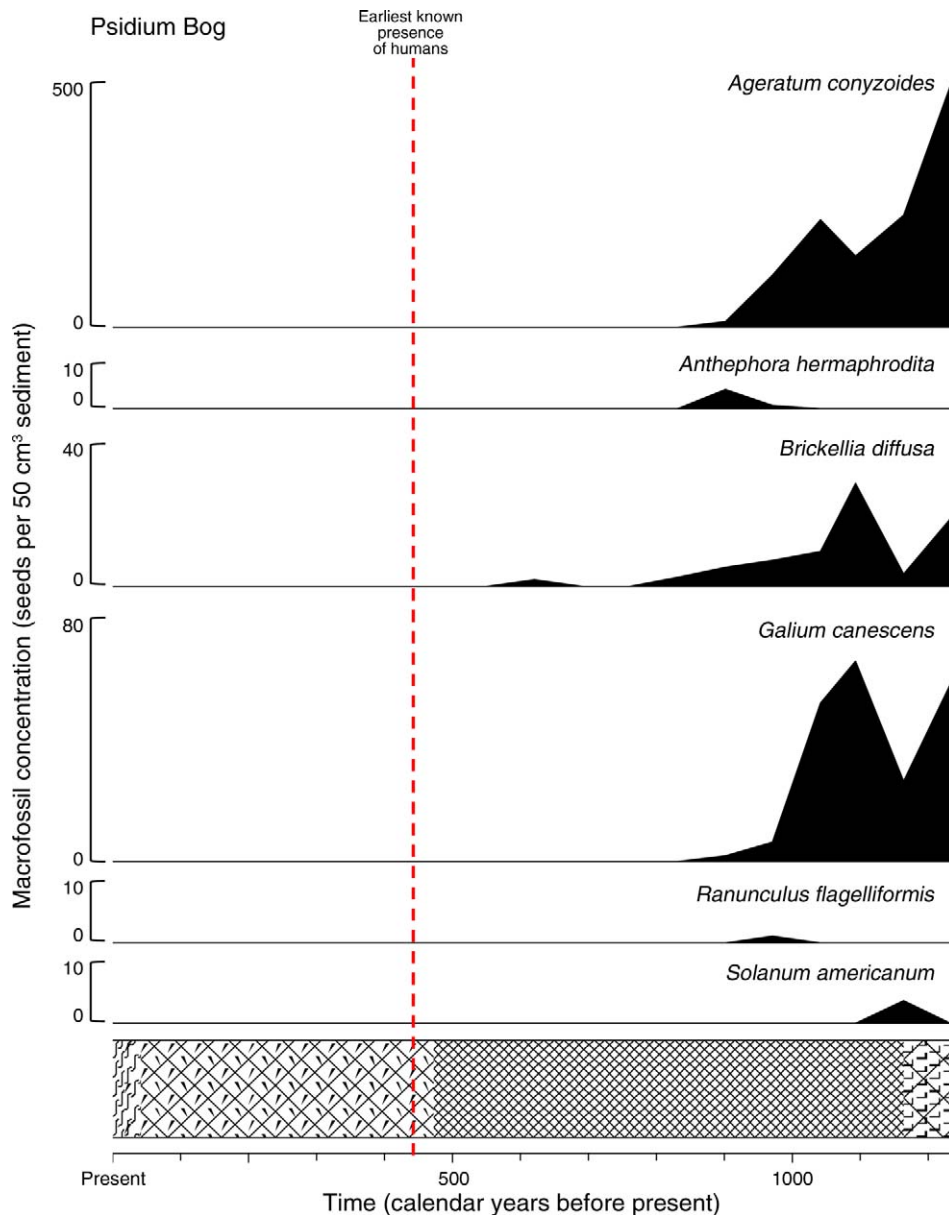


FIG. 2. Macrofossil results for doubtful native species from Psidium bog in the Santa Cruz highlands, Galápagos Islands: concentration diagram of seed fragments $>125 \mu\text{m}$ in 50 cm^3 of sediment. Radiocarbon dates are calibrated calendar years BP. The red dashed line indicates the earliest known presence of humans in the archipelago as a whole.

The Psidium Bog sequence was revealed to span the last 1280 ± 85 cal yr BP (Appendix D), providing evidence of the past occurrence of the doubtful native species, *Brickellia diffusa* (Fig. 2) in addition to the five identified at East Bog. A further additional 34 plant macrofossil species were identified at the site (E. E. D. Coffey, C. A. Froyd, and K. J. Willis, unpublished data). The macrofossil record of the last 100 years at Psidium Bog is dominated by *Sphagnum* plant fragments and little else. Macrofossils of *A. conyzoides* were found to be the most abundant of the doubtful natives, followed by *B. diffusa* and *G. canescens*. *A. hermaphrodita*, *R.*

flagelliformis, and *S. americanum* were all found to have been present at the site in the past, but in low abundance. The majority of the doubtful natives' macrofossils were found during the time period from the opening of the sequence $\sim 1250 \pm 85$ cal yr BP until $\sim 900 \pm 85$ cal yr BP, although all six species occur in the highlands today.

DISCUSSION

During the past five hundred years in which humans have been visiting the Galápagos Islands, introduced species and habitat degradation have been changing the

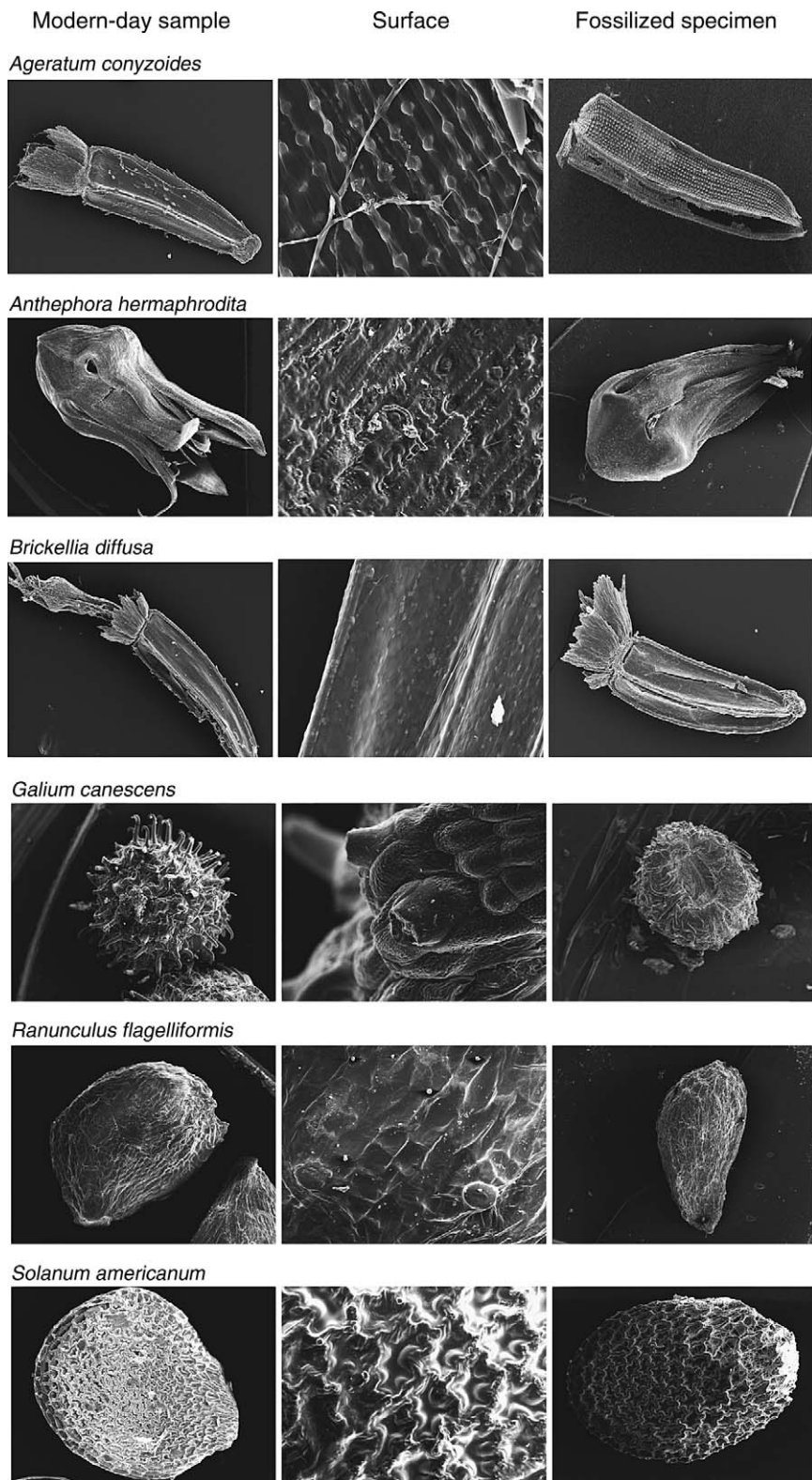


FIG. 3. Scanning electron images for the six doubtful native species. Specimens from modern-day collections were obtained from the Missouri Botanical Garden and the Charles Darwin Research Station Herbarium. All fossilized specimens were taken from sediment samples of East and Psidium Bogs.

islands' natural ecosystems. According to the Biodiversity Vision for the Galápagos Islands (Bensted-Smith 2002) the "ultimate" goal for restoration activities is "the restoration of the populations and distributions of all extant native biodiversity and of natural ecological/evolutionary processes to the conditions prior to human settlement" (Bensted-Smith 2002). One key focus of restoration efforts therefore is to remove known problematic nonnative species (Snell et al. 2002, Jäger et al. 2007). While it may be debatable as to how achievable this goal may realistically be with the current rate at which both humans and the extensive spread of invasive species are changing Galápagos ecosystems, the answer to the following question remains critical for ecosystem restoration: Is a given species native or introduced to the Galápagos archipelago?

Evidence from this study confirms that at least six species of plants (*Ageratum conyzoides*, *Solanum americanum*, *Ranunculus flagelliformis*, *Brickellia diffusa*, *Galium canescens*, and *Antheophora hermaphrodita*) previously considered doubtful natives can be identified as true natives to the Galápagos flora. These species have all been classified by at least one botanical authority as "introduced" or "questionable natives" to Galápagos; however the provenance of each has been questioned as a result either of their presence in accounts of early botanical expeditions, conflicting status designation between authorities, or species traits uncharacteristic of introduced plants (e.g., habitat, lack of use by people, or history as a weed; Appendix E). Each species will be discussed in turn.

The macrofossil findings confirm palynological evidence (van Leeuwen et al. 2008) of the native status of three species, *A. conyzoides*, *R. flagelliformis*, and *B. diffusa*, and reveal that three additional doubtful natives in the highlands are in fact native species (*Solanum americanum*, *Galium canescens*, and *Antheophora hermaphrodita*). Both *G. canescens* and *S. americanum* are known to be native throughout parts of South America. *G. canescens* is a native herb of the Ecuadorian Andean Mountains, typically found at 1000–4500 m above sea level, and according to some accounts is native to the Galápagos Islands (Jørgensen and León-Yáñez 1999); it was formerly considered doubtfully native owing to its apparently late discovery in the islands (Lawesson 1988), an early collection by Charles Darwin (the "*Rubia* sp." of Hooker, see Porter 1980) having been overlooked for many decades. *S. americanum* is considered a pan-tropical weed and can be commonly found in abundance within disturbed areas throughout the Americas and Pacific Islands (Whistler 1988). *S. americanum*-type pollen has been tentatively identified in fossil records from Galápagos, although species-level confirmation could not be made palynologically (C. A. Froyd and J. F. N. van Leeuwen, unpublished data). The macrofossil evidence clearly indicates that the species is native to the Galápagos.

The occurrence of *A. hermaphrodita* in the East bog sequence from over 3000 ± 100 cal yr BP provides important information on native status within the Poaceae family. The Poaceae have the greatest number of species classed as doubtful natives in Galápagos. Identification of Poaceae within the fossil record is often only possible to the family level, however characteristic spikelets observed in the macrofossils allowed for species-level identification of *A. hermaphrodita*. The macrofossil evidence also confirmed van Leeuwen et al.'s (2008) determination of the native status of two species of Asteraceae, another family notoriously difficult to distinguish palynologically. Presence of both *A. conyzoides* (East and Psidium bogs) and *B. diffusa* (Psidium Bog), pan-tropical weed species typically classified as invasive throughout the Pacific Islands (U.S. Forest Service 2006), was found to pre-date human arrival in the Galápagos. The final species for which early macrofossil evidence has been documented is *R. flagelliformis*. The relatively recent discovery of this species in Galápagos in 1972 is suggestive of anthropogenic introduction, but alternatively the non-invasive characteristics of the species indicate it may be native. The macrofossil evidence again confirms palynological evidence (van Leeuwen et al. 2008) of the species' native status.

Of the 62 species classed as doubtful natives in the Galápagos Islands, 38 occur in the high elevation Humid and neighboring Transition vegetation zones. The macrofossil results from this study provide clear evidence that six of these species are native to the Galápagos archipelago. These findings support and confirm results of recent palynological investigations and provide evidence for an additional three doubtful native species to be re-classified as native. Investigations so far have revealed that a total of nine doubtfully native species are confirmed natives: *A. conyzoides*, *S. americanum*, *R. flagelliformis*, *Hibiscus diversifolius*, *B. diffusa*, *G. canescens*, *A. hermaphrodita*, *Spermocoe remota* (= "*Borreria laevis*/*Diodia radula*": Tye and Francisco-Ortega, in press), and *Cuphea carthagenensis*. The earliest fossil records of the six doubtful natives examined here all pre-date human discovery of the islands in AD 1535, and in the case of four of the species (*A. conyzoides*, *S. americanum*, *G. canescens*, *A. hermaphrodita*) were found as early as 4930 ± 100 cal yr BP when the first sedimentary record begins.

Determining the abundance and presence of a species prior to human impact can have direct implications for conservation. For instance, *Hibiscus diversifolius* had been considered an introduced species and a potential habitat transformer in the Galápagos, having caused significant ecological degradation in other regions (U.S. Forest Service 2006). Recent expansion of the species throughout the humid highlands had led land managers to consider the species as invasive and a potential candidate for eradication (van Leeuwen et al. 2008), but palynological investigations indicated that the species is

native. The recent expansion of *H. diversifolius* noted by conservationists may in fact be a re-occupation of former habitats (van Leeuwen et al. 2008).

With the exception of *A. conyzoides* in the East Bog sequence, all of the other doubtful natives examined were more abundant prior to human colonization of the islands, in contrast with their proposed status as introduced species which assumes a recent increase. In the case of *S. americanum* and *G. canescens*, in particular, the historical abundances appear to be well above their current abundance, which is presently considered rare throughout the highlands.

The highly detailed temporal data provided by Psidium Bog, documenting the last 1250 ± 85 cal yr BP, indicate dramatic shifts in species abundances over time. Two climatic shifts occurred during the last 2000 years which may have contributed to this variability. The greatest Holocene variation in El Niño/Southern Oscillation (ENSO) in Galápagos is reported to have occurred during 2000–1000 cal yr BP (Rein et al. 2005, Conroy et al. 2008), bringing increased precipitation and increasing ENSO frequency and intensity. According to Conroy et al. (2009) a second climatic event, a “La Niña-like” pattern, occurred in the tropical Pacific during AD 1250–800, with cooler sea surface temperatures (SSTs) resulting in cooler and dryer terrestrial conditions for the islands (Conroy et al. 2009). The overall decline of all six doubtfully native species in the Psidium Bog sediment around 900 ± 85 cal yr BP, as well as the decline in *S. americanum* during the same period in the East Bog sequence, coincides with this and may be attributable to increasingly drier climate and changing habitat conditions surrounding the bogs which may have been less favorable to these species. The six doubtful native species do not occur in the Psidium Bog sequence post-dating human arrival in the Galápagos.

The variability throughout the East Bog core (Fig. 1) provides a longer temporal picture. Examining *A. conyzoides* there were two major declines during $1220\text{--}970 \pm 50$ cal yr BP and $4100\text{--}3100 \pm 90$ cal yr BP, otherwise the abundance remained fairly consistent during the last 5000 years BP. The decline during $1220\text{--}970 \pm 50$ cal yr BP (AD 980–720) coincides with the La Nina-like climatic period of AD 1250–800 (Conroy et al. 2009).

Interestingly, *S. americanum* shows a clear temporary increase in abundance in East Bog at 950 ± 50 followed by a dramatic decline at 350 ± 90 cal yr BP. *A. conyzoides* is also abundant throughout this period. These patterns could be due to a transition in the overall species composition surrounding the caldera. A lithological transition from lake sediment to decomposed *Sphagnum* peat indicates a shift from standing open water lake-like conditions to drier *Sphagnum* peat bog conditions which took place approximately 680 ± 50 cal yr BP. The drying of a lake would open the area for non-aquatic species to expand, thus temporarily increasing

available habitat. Declining abundances in more recent times, as noted in the Psidium Bog sequence, may be the result of additional changes resulting from human impact. Three peaks of abundance in the *G. canescens* populations occurred during the periods of decline of *A. conyzoides*, potentially indicating a change in species composition. It is possible that the decline of the abundant *A. conyzoides* provided an opening in the habitat for additional species or alternatively, that climatic conditions were more favorable toward *G. canescens* during this period.

The abundance of the remaining two species in the East Bog sequence, *A. hermaphrodita* and *R. flagelliformis*, did not fluctuate greatly, as the populations remained small. Both disappeared from the fossil record by around 2100 ± 60 cal yr BP. The timing of the complete departure from the fossil record of *A. hermaphrodita* and *R. flagelliformis* also corresponds to the changes in the ENSO patterns previously described (Conroy et al. 2008), although the species still remain present in low abundance in the highlands today. Similar results were reported for *R. flagelliformis* in the palynological record (van Leeuwen et al. 2008). Due to the difficulty distinguishing Poaceae pollen, *A. hermaphrodita* cannot be compared with the macrofossil results.

Addressing the fluctuations in the abundance of these species provides important information on their historical stability. It is apparent from the data that the doubtful natives found in the paleo record have all experienced declines, some more dramatic than others, since the arrival of humans. The reasons for these shifts could be related to the impacts humans have had on the ecosystems or natural shifts and variability in species over time.

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APPENDIX A

Maps of the study sites (*Ecological Archives* E092-068-A1).

APPENDIX B

Field site photographs of East Bog and Psidium Bog taken in January 2009 (*Ecological Archives* E092-068-A2).

APPENDIX C

Detailed description of sediment stratigraphy and chronology for both East Bog and Psidium Bog (*Ecological Archives* E092-068-A3).

APPENDIX D

A table showing all radiocarbon dates for both East Bog and Psidium Bog (*Ecological Archives* E092-068-A4).

APPENDIX E

A table showing current and historical species classifications for six doubtfully native plant species (*Ecological Archives* E092-068-A5).