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Lake or bog? Reconstructing baseline ecological conditions for the protected Galápagos *Sphagnum* peatbogs

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ABSTRACT

This paper documents the first 10,000 year old plant macrofossil record of vegetation changes on the central island of Santa Cruz, providing information on *Sphagnum* bog vegetation patterns, local extinction of key taxa, and temporal successions in the Galápagos humid highlands. Vegetation change is reconstructed through examination of Holocene sedimentary sequences obtained from three *Sphagnum* bogs located within volcanic caldera forming the high elevation central ridge system of Santa Cruz Island. Results indicate that these specialized *Sphagnum* bog ecosystems are dynamic and have undergone considerable changes in vegetation composition, transitioning from diverse hygrophilous herbs and submerged aquatic ecosystems to drier *Sphagnum*/*Pteridium* bog systems, during the last 10,000 cal yr BP. Additionally a new aquatic genus previously undocumented on the islands, *Elatine*, was discovered at two of the study sites, but it is now extinct on the archipelago. Some of the observed vegetation successions may have been driven by climatic shifts occurring within the eastern equatorial Pacific (EEP). Other drivers including anthropogenic change are also considered significant over the last hundred years, placing strain on this naturally dynamic system. This study helps reveal patterns of change in the humid highlands over the last 10,000 cal yr BP regarding vegetation variability, climatic shifts, the historical influence of fire, tortoise disturbance, and recent anthropogenic impacts on the island.

1. Introduction

Theories pertaining to restoration ecology often identify the need to address both temporal variation and spatial diversity inherent in natural ecosystems (Parker, 1997; Wilkinson et al., 2005). Additionally, knowledge of baseline ecological conditions is needed to develop key conservation strategies and local management goals, providing important qualitative data required for understanding previous variability and diversity within ecosystems (Willis et al., 2007). Palaeoecological reconstructions from fossils assemblages provide valuable information about changes in climate (Colinvaux, 1972; Conroy et al., 2008, 2009), environmental factors (Correa-Metrio et al., 2010), species provenance (van Leeuwen et al., 2008; Coffey et al., 2011) and human impacts on the vegetation (Burney, 1997; Armesto et al., 2010).

The Galápagos Islands, with their unique natural diversity are considered one of the world's conservation 'hotspots' (Conservation International, 2005). However, temporal baseline data for many of the specialized vegetation assemblages on the islands are poorly understood. In this study we examine the baseline conditions of the *Sphagnum* bog communities in the humid highlands of Santa Cruz Island, Galápagos.

Five main climatic formations have been recognized throughout the Galápagos archipelago, each a product of climate and topography: littoral, dry, transition, humid, and high-altitude dry zones (Tye et al., 2002; Trueman and d'Ozouville, 2010). All but the high-altitude dry zone occur on the central island of Santa Cruz, with a maximum elevation of 864 m on Mount Crocker (Trueman and d'Ozouville, 2010). Within the upper most humid zone, four major vegetation formations have been identified based on the dominant vegetation type (Tye and Francisco-Ortega, 2011): *Scalesia* (180–280 m a.s.l. (above sea level)), *Zanthoxylum* (280–420 m a.s.l.), *Miconia* (420–570 m a.s.l.), and fern-sedge (570–864 m a.s.l.) (Tye et al., 2002). The fern-sedge formation in particular is rich in endemic and threatened taxa and has been the focus of recent studies (Jäger et al., 2007, 2009; van Leeuwen et al., 2008; Jäger and Kowarik, 2010; Coffey et al., 2011). Species once presumed invasive or non-native, such as *Hibiscus diversifolius* and *Ranunculus flagelliformis*, have since been reclassified as native to the highland

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ecosystems (van Leeuwen et al., 2008; Coffey et al., 2011). This formation also supports specialized *Sphagnum* peatbogs growing within volcanic caldera.

The humid and very humid zones have experienced the highest percentage of anthropogenic degradation in the Galápagos, either through direct changes, e.g. habitat modification, or indirect e.g. introduction of invasive species and fire (Watkins and Cruz, 2007). Seventy-six percent of the fern-sedge formation, for example, is considered transformed (Watson et al., 2010). Current Galápagos National Park regulations protect the Santa Cruz fern-sedge formation from direct human-induced modification such as agricultural expansion; however, the greatest threat to this formation is the negative impact of invasive species.

Recent studies have documented the negative impacts invaders such as *Cinchona pubescens* have had on native vegetation and particularly endemic species within the fern-sedge formation, with up to an 82% reduction of native species cover over a seven year period (Jäger et al., 2007, 2009). Cover of the endemic herb *Pilea baurii*, for example, was reduced by 98% (Jäger et al., 2009). In addition to dramatic declines in diversity and cover of rare and endemic species of highland plants, habitat transformations have also impacted endangered animal species, such as the critically endangered endemic Galápagos Petrel, *Pterodroma phaeopygia*, which nests exclusively in the humid highlands (Cruz-Delgado et al., 2009).

It is also within this unique fern-sedge formation of Santa Cruz Island that the only remaining *Sphagnum* peatbogs in the Galápagos can be found. Peatbog depressions were formerly recorded on the island of Pinta in 1976 (Adsersen, 1976; Hamann, 1979) but, have since been destroyed by goats (personal observation 2007). The temporal variability and resilience of the fern-sedge formation communities on Santa Cruz are unknown (Jäger and Kowarik, 2010) and information is required in order to develop a restoration model for these Galápagos highland plant communities (Wilkinson et al., 2005). Therefore, a key element of this study is to help establish baseline data for the humid highlands, providing a benchmark and basis for conservation planning aimed at preservation of biological diversity on the Galápagos Islands (Bensted-Smith, 2002).

The aims were to address the following questions: (1) How old are the highland peatbog communities on Santa Cruz? (2) What is the natural variability of the peatbogs through time in response to climate change and other environmental factors? (3) How resilient are these communities to human impact since the first arrival of people in AD 1535?

2. Regional setting

The Galápagos Islands are comprised of thirteen large islands (greater than 10 km^2) and 128 smaller islets and rocks, located approximately 950 km west of South America in the eastern Pacific (Latitude S 0° 38′ and Longitude W 90° 19′) (Fig. 1a). The central island Santa Cruz, where this study was conducted, has a land area of 986 km^2 (Jackson, 1993; Kricher, 2006).

The characteristic feature of the fern-sedge vegetation formation, which is widespread in the highlands of Santa Cruz and San Cristóbal, is the complete lack of native tree species. Occurring between 570 m and 865 m a.s.l. the region experiences intense moisture from the nearly persistent inversion layer that forms during the cool season between June and December. A wide variety of plant communities are supported (Itow, 2003; Hamann, 2011). For example, the tree-fern *Cyathea weatherbyana* forms groves in ravines and other sheltered habitats; *Pernettya howellii* dominates heath-land communities; herb communities are composed of species including *Jaegeria crassa*, *Lobelia xalapensis*, *P. baurii*, *Hypericum uliginosum*, *Centella asiatica*, and *Polygonum opelousanum*; and grass and sedge communities include *Paspalum conjugatum*, *Trisetum howellii*, *Eleocharis* spp., *Cyperus* spp., *Scleria* spp., and *Rhynchospora* spp. The most widespread community is composed of pteridophytes including *Pteridium arachnoideum*, *Polypodium tridens*, *Blechnum polypodioides*, *Blechnum occidentale*, *Nephrolepis pectinata*, *Pityrogramma calomelanos*, *Lycopodium clavatum*, *Lycopodiella cernua*, and *Thelypteris* spp. (Wiggins et al., 1971). The soils are relatively deep throughout the area. Fens and raised *Sphagnum* peatbogs are scattered across this formation (Itow and Weber, 1974). Fens and ephemeral wetlands develop primarily during the cool season in shallow depressions supporting species such as *Sphagnum cuspidatum*, *Eleocharis* spp., and *Polygonum* spp. *Sphagnum* peatbogs, composed of *S. erythrocalyx* and *S. cuspidatum*, are located in the calderas of inactive volcanoes (Fig. 1a and b) (Wiggins et al., 1971). Thick mats composed of *Sphagnum*, *Gleichenia* spp., *Blechnum* spp., *P. howellii*, *Lycopodium clavatum*, and *Lycopodiella cernua* cover the surfaces of the peatbogs.

3. Materials and methods

3.1. Sediment sampling

Sediment cores were collected from three *Sphagnum* bogs (Fig. 1b). All are situated above 700 m elevation in cinder cone craters, on the southern slope of the Cerro Crocker ridge, with a maximum of distance between the sites of 1.24 km. The three bogs, identified as "East Bog" (S 0° 38′ 45″, W 90° 19′ 03″, 739 m a.s.l.), "Psidium Bog" (S 0° 38′ 38″, W 90° 19′ 37″, 809 m a.s.l.), and "Pernettya Bog" (S 0° 38′ 55″, W 90° 19′ 42″, 782 m a.s.l.) were all similar in area (between ~1000 and 2300 m^2) and vegetation formation type. No perennial streams flow into the craters; precipitation throughout the year maintains the moisture in the *Sphagnum* bogs.

Continuous sedimentary sequences were extracted in 1 m segments using a modified Livingstone Piston Sampler (Wright et al., 1984) (Table A1). Sedimentary samples were taken from the littoral/edge of the bog, where macrofossils often occur in larger concentrations (Birks, 2001).

3.2. Age-depth determination

Radiocarbon-dating, using both AMS (accelerator mass spectrometry) and conventional (gas proportional counting) techniques, were used to establish chronologies for the three sediment sequences (Table A2). The dates were calibrated to calendar years before present (cal yr BP) using the Southern Hemisphere terrestrial calibration curve SHCa1 04 (McCormac et al., 2004) in the program Clam 1.0.2 (Blaauw, 2010) in R version 2.12.1 (R Development Core Team, 2010). Linear interpolation was used to develop age-depth models for each sequence between the ^{14}C dated sections. Age-depth results were analysed and displayed using the Clam 1.0.2 (Blaauw, 2010) software program.

3.3. Laboratory analysis

Lithological descriptions follow Troels-Smith classification (Troels-Smith, 1955) (Table A3, Figs. A1–A3). The organic content of the cores was determined by loss-on-ignition (LOI) at 550 °C (Dean, 1974). Employing methodology similar to Birks (2001), 50 cm^3 sediment samples were taken for macrofossil analysis at 8 cm intervals. The samples were examined using a Nikon SMZ800 stereo-microscope, where the total number of fossilized seeds/fruits, seed fragments, and plant parts >125 μm for each sample (up to 2000 per species) were tallied (*Sphagnum* fossils were counted as leaves and leaf fragments attached to stems). The sample material was simultaneously examined for charcoal and tephra particles which were counted and assigned to size classes (</>1 mm).