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ORIGINAL ARTICLE

Influences of sea level changes and volcanic eruptions on Holocene vegetation in Tonga

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Abstract

Here, we investigate Mid- to Late-Holocene vegetation changes in low-lying coastal areas in Tonga and how changing sea levels and recurrent volcanic eruptions have influenced vegetation dynamics on four islands of the Tongan archipelago (South Pacific). To investigate past vegetation and environmental change at Ngofe Marsh ('Uta Vava'u), we examined palynomorphs (pollen and spores), charcoal (fire), and sediment characteristics (volcanic activity) from a 6.7-m-long sediment core. Radiocarbon dating indicated the sediments were deposited over the last 7700 years. We integrated the Ngofe Marsh data with similar previously published data from Avai'o'vuna Swamp on Pangaimotu Island, Lotofoa Swamp on Foa Island, and Finemui Swamp on Ha'afeva Island. Plant taxa were categorized as littoral, mangrove, rainforest, successional/ disturbance, and wetland groups, and linear models were used to examine relationships between vegetation, relative sea level change, and volcanic eruptions (tephra). We found that relative sea level change has impacted vegetation on three of the four islands investigated. Volcanic eruptions were not identified as a driver of vegetation change. Rainforest decline does not appear to be driven by sea level changes or volcanic eruptions. From all sites analyzed, vegetation at Finemui Swamp was most sensitive to changes in relative sea level. While vegetation on low-lying Pacific islands is sensitive to changing sea levels, island characteristics, such as area and elevation, are also likely to be important factors that mediate specific island responses to drivers of change.

KEYWORDS
anthropogenic impacts, human impacts, paleoecology, pollen analysis, Polynesia, sea level, tephra, Tonga

1 | INTRODUCTION

Pacific islands are subject to volcanic eruptions and sea level change, which may put their populations and ecosystems at risk (Cronin et al., 2004; Nakicenovic et al., 2000). The January 2022 Hunga Tonga-Hunga Ha'apai volcanic eruption, and associated tsunami inundation of parts of Tonga, exemplifies the need to improve our understanding of how island ecosystems respond to environmental dynamics. This research analyses four paleoecological records from Tonga, one new in this study and three extant records, to quantify how vegetation (littoral, mangrove, rainforest, successional/ disturbance, and wetland; Table 1) responded to both sea level changes and volcanic eruptions over the last 5000–7000 years.

It is well established that the timing and sources of past volcanic eruptions can be derived from tephra layers preserved in the stratigraphy of sediment records (Lowe, 2011). Such layers allow researchers to identify how ecosystems responded to volcanic events, especially when recovery periods exceed the timescales of modern observations, that is, centuries rather than decades. Evidence for the impacts of volcanic eruptions on vegetation from other ecosystems worldwide indicates variable responses, recovery times and initial conditions (Strandberg et al., 2023). For example, in Ecuador, a paleoecological reconstruction showed an increase in grass pollen and a decrease in forest pollen, presumably indicating a shift in vegetation cover (Montoya et al., 2021), while in Chile, Fesq-Martin et al. (2004) recorded a primary succession sequence. In other cases, impacts on vegetation may not be detected at all (e.g., Gosling et al., 2020), they may be brief, for example, lasting up to a few decades (Lotter & Birks, 1993; Urrutia et al., 2007) or longer lasting, for example, several hundred years (Fesq-Martin et al., 2004).

Evidence of past volcanic activity in Tonga includes a stratigraphic tephra and pollen record from Lotofoa Swamp, Foa, Ha'apai group (Figure 1), which shows an increase in mangrove taxa *Excoecaria* (Tongan name feta'anu) for ~3000 years following an eruption ~3840 cal. years BP (Flenley et al., 1999). However, it is difficult to disentangle the effect of volcanic eruptions from those of relative sea level rise (RSL) and other environmental changes.

Ecosystems in Tonga have also been influenced by changes in RSL; for example, a Holocene sea level high stand was identified using sediment cores from Folaha Lagoon, Tongatapu and Avai'o'vuna Swamp, Vava'u and dated between ~5000 and 2000 cal. years BP (Ellison, 1989; Fall, 2005). Sea levels reached near-present levels in the South Pacific by ~7300 cal. years BP, then were up to 2 m higher than present by the Mid-Holocene, ~4000 cal. years BP, before falling towards present day levels thereafter (Nunn & Peltier, 2001). Similar patterns of change have been identified from modelled RSL changes from Tongatapu (Fukuyo et al., 2020). Changes in sea level altered coastal environments, resource availability, and the size and shape of the islands (Margalef et al., 2018; Nunn, 2009). In particular, mangrove vegetation zones retreated and advanced with sea level rise and fall (Ellison, 1989). Mangrove species with narrow elevation ranges (~0.4 m), including those with a preference for the landward zone (e.g., *Nypa fruticans*), may also be more at risk than those with broad ranges, for example, *Bruguiera gymnorhiza* (tongo lei) (Ellison et al., 2022). In addition, sediment accretion rates show that mangrove communities in tropical coastal regions are not able to keep pace with projected future sea level rise (Saintilan et al., 2020). Despite the importance of RSL changes, there has been limited regional analysis to determine how littoral vegetation, occurring along the shore or landward of mangrove forests, for example, *Barringtonia* (futu), *Casuarina* (toa), and *Pandanus* (fafa), and rainforest taxa, for example, *Syzygium* (fekika) and *Dysoxylum* (mo'ota), may be impacted by changes in sea level.

Using the most complete records of RSL and tephra deposition available, we investigated how changes in these drivers have impacted the vegetation of Tonga during the Mid- and Late-Holocene, also taking into consideration the role of island size and elevation. We first describe a new paleoecological record from Ngofe Marsh on the island of 'Uta Vava'u (Vava'u group). We then present a regional analysis of four sites: Ngofe Marsh and three published records from Tongan islands (Fall, 2005; Flenley et al., 1999).

TABLE 1 List of the six vegetation groups used to classify the fossil pollen taxa: littoral, mangrove, rainforest, successional, or disturbance, wetland, and others.

Vegetation group	Description and ecology	Typical fossil pollen taxa
Littoral	Includes coastal back-beach herbs, shrubs, and trees, also plants of coastal raised rocky shorelines. These are usually narrow vegetation zones affected by marine influences such as part-saline groundwater, reduced freshwater availability and perhaps salt spray. Taxa are often water dispersed (Fall & Drezner, 2011)	*Barringtonia*, *Casuarina*, *Cocos nucifera*, and *Pandanus*
Mangrove forests	Taxa growing around mean tide elevations up to high tide. Taxa are mostly water dispersed (Fall & Drezner, 2011)	*Acrostichum*, *Excoecaria*, *Rhizophora*, and Rhizophoraceae
Rainforest type	Includes coastal forest (further inland than the littoral forest), lowland forest, and montane forest with canopies up to 30m in height. According to Fall (2010), this was the dominant vegetation type before human arrival in most areas, apart from those that have experienced recent volcanic activity (Whistler, 1992)	Anacardiaceae, *Canarium*, *Diospyros*, *Dysoxylum*, *Elaeocarpus*, Myrtaceae, and Sapotaceae
Successional, or disturbance-adapted secondary forest	Includes managed land, secondary scrub, and secondary forest. Many species are considered anthropochores	*Homalanthus*, *Macaranga*, *Plantago* and *Trema*
Wetland	This includes inland freshwater wetlands (which may be close to the coast) and upland wetlands that are dominated by herbaceous taxa	Cyperaceae, *Polygonum*, *Potamogeton*, *Stenochlaena*, and *Typha*
Other	Includes grasses, lowland volcanic scrub, upland scrub, and taxa which cannot be otherwise classified due to taxonomic uncertainty/ lack of botanical information	Monolete fern spores, Poaceae, and trilete fern spores

Note: Information on the vegetation classifications and description is inferred from on contemporary vegetation ecology based on Whistler (1992) and Ellison (1990).

2 | METHODS

2.1 | Study sites

The Tongan archipelago lies on the eastern margin of the Asia-Australian Plate, which is uplifting as the Pacific Plate subducts under it; this causes volcanic activity (Crane, 1979). The 169 islands in Tonga mostly consist of raised limestone or coral sand cays. The larger islands, such as Tongatapu, have fertile soils due to nutrient inputs from ash falls over time (Roy, 1990). Raised limestone karstic islands are permeable and have freshwater lenses (Roy, 1990); their surface elevation is controlled by sea level position (White & Falkland, 2010). The climate in Tonga is mild marine tropical, and South Pacific trade winds dominate for most of the year (Fall, 2010). Precipitation averages around 2340mm per year and the average annual temperature is 23.5°C (Thompson, 1986).

Tonga is part of the South-Western Pacific, Indo-Melanesian floristic area (van Steenis, 1979). In a review, Fall and Drezner (2020) identified 1020 vascular plant species in Tonga with 450 of these being native. Fewer than 2% of the 1020 species identified are endemic (Fall & Drezner, 2020).

2.2 | Coring site at Ngofe Marsh on ‘Uta Vava'u island

Ngofe Marsh is a land-locked wetland on the island of Uta' Vava'u, in the Vava'u island group (18°39′49.27″S 174°02′35.57″W; 4ma.s.l.). Recently, the flora of Ngofe Marsh has been dominated by the sedges *Eleocharis dulcis* (kutu) and *Lepironia articulata* (kutu kofe), and the swamp tree *Erythrina variegata* (ngatae; Fall, 2010). In May 2017, a 670-cm long sediment core was retrieved from Ngofe Marsh from the center of the basin. The core segments were collected using a 5-cm-diameter Russian peat corer with a 50-cm-long sampling chamber. The cores were retrieved with 10-cm overlaps to avoid missing any part of the sequence, boxed carefully to avoid movement during transit, and transported back to the UK within 48h after collection. All cores were stored at 5°C at the University of Southampton cold core storage facility, UK.

2.3 | Radiocarbon dating for Ngofe Marsh

Three macrofossil and three bulk-sediment samples were dated using AMS (accelerator mass spectrometry) radiocarbon techniques at the SUERC NERC Radiocarbon Laboratory. Radiocarbon dates were calibrated using the Southern Hemisphere calibration curve (Hogg et al., 2020). The age-depth model for Ngofe Marsh was created using the *rbacon* package in R Studio (Blaauw & Christen, 2011; R Core Team, 2017; RStudio Team, 2015; Table S2).

2.4 | Palynomorph and charcoal extraction, identification, and counting

Sixty-one core sediment subsamples were prepared for analysis following standard procedures (Erdtman & Wodehouse, 1944) giving an approximate resolution of one sample per 120 years for the Ngofe Marsh main core. Subsamples of 1-cm^3 volume

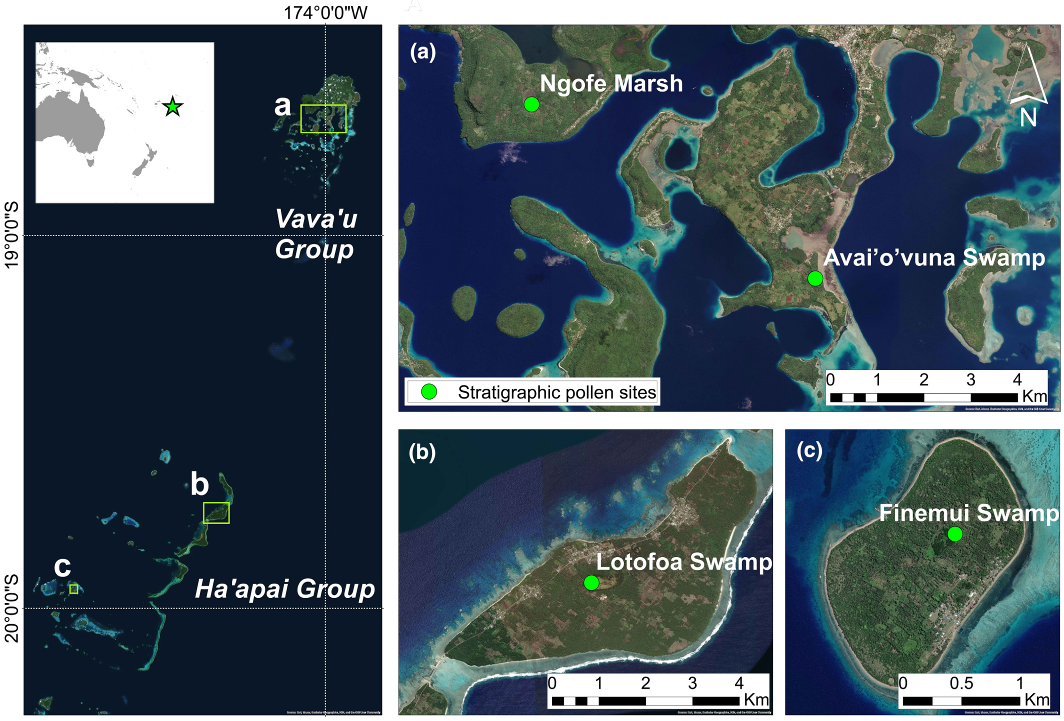

FIGURE 1 Left panel: the Northern Tongan island groups and locations of study sites. The stratigraphic pollen sites are; (a) Ngofe Marsh on 'Uta Vava'u Island (this study) and Avai'o'vuna Swamp on Pangaimotu Island (Fall, 2005), (b) Lotofoa Swamp on Foa Island, and (c) Finemui Swamp on Ha'afeva Island (Flenley et al., 1999). Satellite imagery is from ESRI (2022).

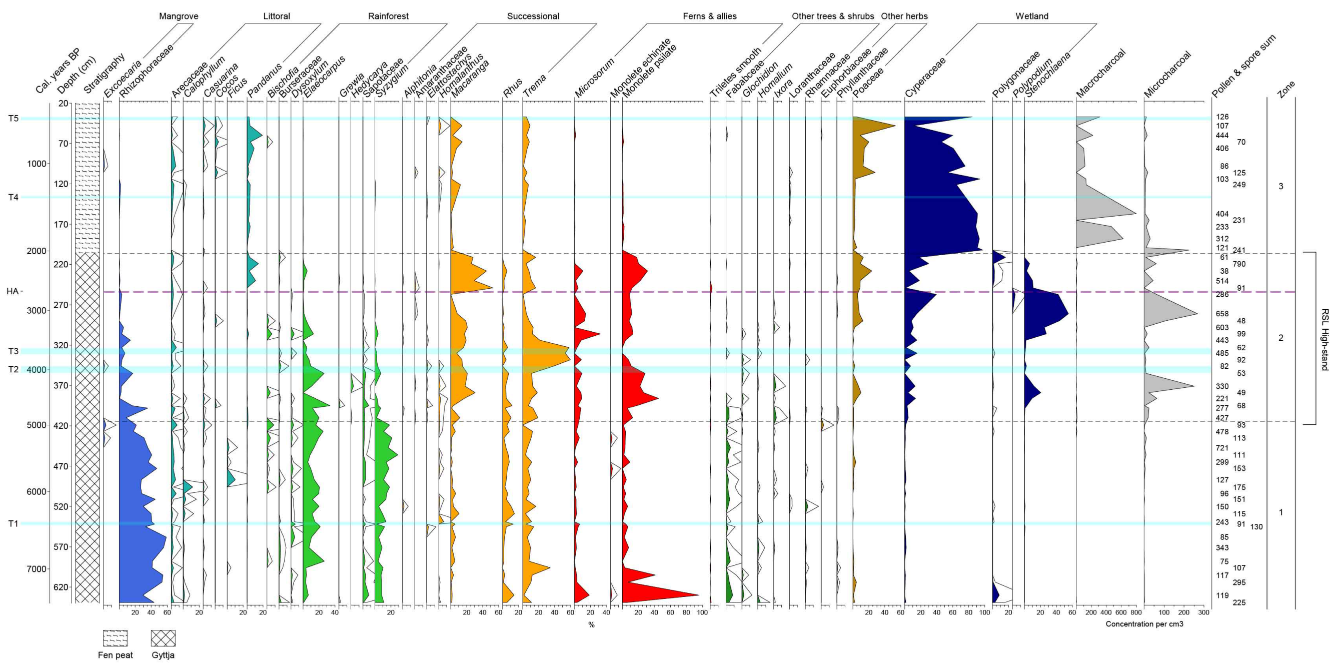

FIGURE 2 Pollen, spores, and charcoal from Ngofe Marsh; pollen and spore percentages display taxa >2%. Pollen and fern spores are included in the total sum. Uncertain identifications have been omitted from the CONISS calculations (Grimm, 1987). Zonation is based on the CONISS dendrogram and represented as fine dashed lines. Tephra layers are indicated as T1–T5 on the left-hand side and are shaded in blue. The potential timing of human arrival (HA) is represented as a purple dashed line based at ~2670 cal. years BP. The timing of the Mid- and Late-Holocene RSL high stand, according to Fukuyo et al. (2020), is shown on the right-hand side.

were taken from the core and *Lycopodium* tablets (batch #3862, $n = 9666$ and batch #140119321, $n = 19{,}855$) were added in order to calculate charcoal concentrations (Stockmarr, 1971). See the Data S1 for a detailed description of the pollen preparation methods. Pollen grains were counted at 400× magnification with detailed identification and photography of grains at 1000× magnification (Figure S4). Pollen identification was carried out using the pollen reference collection of Prof. John Flenley stored at the Department of Geography, Geology and Environment, University of Hull, and three pollen keys (ANU, 2007; Gosling et al., 2013; Poliakova & Behling, 2016). The pollen percentage diagram was created in Tilia 2.0.41, and pollen assemblage zones were determined using CONISS, a cluster analysis technique included in Tilia (Grimm, 1987, 1990).

To investigate fire history around Ngofe Marsh, we counted micro- and macrocharcoal fragments at ~10-cm intervals. Microcharcoal particles (<125 μm), indicating a regional fire signal, were identified in the pollen slides as opaque, black, and angular fragments. The microcharcoal particles were counted alongside pollen grains and the exotic *Lycopodium* spike across regularly spaced transects on each slide (Wang et al., 1999). Macrocharcoal samples, counted to reconstruct local fire history, were prepared by sieving 1-cm^3 sediment samples at 125 μm and retaining the >125-μm fraction; this was bleached with 6% H_2O_2 until the reaction stopped. All macrocharcoal fragments in a sample were counted using a stereo microscope.

2.5 | Paleoecological information of the additional pollen records

We augmented the Ngofe Marsh pollen data with three pollen datasets: (1) Avai'o'vuna Swamp, a coastal wetland on Pangaimotu Island in the Vava'u island group (Fall, 2005), (2) Finemui Swamp on the small island of Ha'afeva, and (3) Lotofoa Swamp on the island of Foa (Flenley et al., 1999; Figure 1). All sites are relatively low lying (<7 m a.s.l.) and hence have the potential to be impacted by changes in RSL. For these sites the age-depth models were recalibrated using the SHCal20 calibration curve (Hogg et al., 2013). We digitized the pollen percentage diagrams and core stratigraphies from Lotofoa Swamp (basal age 7200 cal. years BP) and Finemui Swamp (basal age 5200 cal. years BP) of Flenley et al. (1999) using ImageJ software (Schneider et al., 2012). We used the original counts from Avai'o'vuna Swamp (basal age 4800 cal. years BP) from Fall (2005).

2.6 | Vegetation groupings

We classified all pollen taxa into one of the following groups: littoral, mangrove forest, rainforest, successional/ disturbance, wetland, and other, see Table 1; following Whistler (1992) and Ellison (1990). Mangrove taxa have been listed previously for Tonga (Ellison, 1990), and littoral taxa were identified with reference to the flora of Malinoa island (21°2′12.33″S 175°7′43.84″W). The census flora list of Malinoa island was used as an example of a littoral habitat ecosystem due to the island's small (~0.66 km^2) size and low elevation (<7 m.a.s.l.). Genus and family names with the prefix cf. were omitted. Uncertain pollen and spore identifications also were omitted. Taxa with the notation "comp." (favorably comparable) and "sim." (similar to) were included (Benninghoff & Kapp, 1962).

2.7 | Sediment and tephra analysis

We used two methods to detect tephra falls from volcanic eruptions: (1) tephra content and tephra shard geochemistry and (2) the stratigraphic description from sedimentary sequences.

2.7.1 | Tephra content and tephra shard geochemistry

For Ngofe Marsh, we determined the sediment elemental variations and Ti/incoherent-scatter using an Itrax core scanner (BOSCORF, National Oceanography Centre) using established procedures (Croudace et al., 2019). The scanner used a Mo-X-ray tube and analysis was carried out at a 200-μm step-size and a dwell time of 30 s. We also used magnetic susceptibility to detect layers with higher magnetism that might include potential tephra layers with a predicted higher Fe-Ti content/mineralogy. These data were obtained using a Bartington MS2 scanner (Dearing, 1994). Sections of the cores that displayed relatively higher values of magnetic susceptibility and Ti/incoherent-scatter (Tephra layers T1–T5; determined from Itrax scanner, see Figure S3) were subsampled and analyzed for tephra content and tephra shard geochemistry. See the Data S1 for the tephra geochemistry method.

2.7.2 | Stratigraphic descriptions of sedimentary sequences

For Lotofoa Swamp (Figure 1b), and Finemui Swamp (Figure 1c), we used the stratigraphic description from Flenley et al.'s (1999) study to indicate the locations of tephra layers. For Avai'o'vuna Swamp (Fall, 2005), no tephra layers were identified during the analysis of sediment cores. However, given the close proximity (6 km) of the two sites, we match the Ngofe Marsh tephra dataset to the Avai'o'vuna sedimentary sequence (see Table S3).

2.8 | Holocene sea level change

Sea level change for the Tongan archipelago over the past 6000 years was obtained from Fukuyo et al. (2020). The model output we digitized to be used in the linear models was with lithospheric thickness of 65 km, lower mantle viscosity of 2 (10^{20} PaS), and upper mantle viscosity 1 (10^{22} Pa S). The same sea level model was used for all four sites.

2.9 | Statistical analysis

The analyses are based on percentage data of the vegetation groups (Table 1), in which the "other" group was removed and the data for the five remaining vegetation groups were rescaled to 100%. For the Ngofe Marsh pollen record, Cyperaceae, belonging to the wetland habitat group, dominated the pollen record (up to 80% of the pollen and spore sum), potentially masking other interesting shifts within habitat groups, for this reason Cyperaceae was removed from the Ngofe Marsh analysis. Pollen percentage data were log-transformed to normalize distributions. Linear models were used to investigate the relationship between the pollen taxa from littoral, mangrove, rainforest, successional/ disturbance, wetland vegetation groups, RSL, and volcanic eruptions (tephra) at each site separately. The tephra variables consist of 0 and 1s for absence or presence of tephra layers, respectively. Tephra layers were assigned dates from the age-depth models (Figure S2). Temporal changes of vegetation groups were visualized for each island using local polynomial regression fitting (Figure 3).

3 | RESULTS

3.1 | Pollen, spores and charcoal records for Ngofe Marsh

The core stratigraphy, radiocarbon dates (Table S2), and calibrated age-depth models (Figure S2) are presented in the supplementary information. The pollen diagram (Figure 2) was divided in three zones based on CONISS cluster analysis (Grimm, 1987).

3.1.1 | Pollen assemblage zone one: 639–414 cm (7440–4920 cal. years BP)

This pollen zone contains 24 samples. Mangroves (Rhizophoraceae 31%), rainforest (*Elaeocarpus*-type 12%, *Syzygium* 9%), disturbance taxa (*Trema* 12%), and ferns (monolete fern spores 5%) dominate the record. A ~300-year peak in *Trema* starts at around 3900 cal. years BP and is associated with a tephra layer. There are also minor occurrences of coastal taxa such as *Terminalia*-type (1%) and rainforest taxa such as Arecaceae, Burseraceae, *Calophyllum*, Fabaceae, *Homalium*, *Ixora*, Melastomataceae, Meliaceae, and Sapotaceae. The disturbance taxa *Homalanthus* and *Rhus* are found in abundances of <1% and 5%, respectively. Macro- and microcharcoal concentrations are low (<1 fragment per cm^3 and ~15,700 fragments per cm^3, respectively).

3.1.2 | Pollen assemblage zone two: 414–206 cm (4920–2040 cal years BP)

This pollen zone contains 22 samples. There are evident peaks in *Trema* 17%, *Stenochlaena* fern spores 17%, *Macaranga* 15%, monolete fern spores 14%, and cultivated Poaceae grains >40 µm 2%. The primary rainforest taxa *Elaeocarpus* and *Syzygium* decrease to 4% and 1%, respectively. The successional taxon *Rhus* also decreases to 1%. Microcharcoal concentrations increase to around 725,000 fragments per cm^3. Macrocharcoal concentrations remain low (~2 fragments per cm^3) or zero.

3.1.3 | Pollen assemblage zone three: 206–44 cm (2040–430 cal. years BP)

This pollen zone contains 15 samples and coincides with reed peat in the stratigraphy. There is increased pollen from Cyperaceae 80%, *Pandanus* 17%, *Macaranga* 14%, and Poaceae 13%. For most samples, pollen from rainforest taxa and mangroves is absent. Microcharcoal concentrations are lower (140,000 cm^{-3}) than in pollen assemblage zone two, but macrocharcoal is present with high concentrations of ~100–600 fragments per cm^3.

3.2 | Tephra falls from volcanic eruptions

Analysis of samples (T1–T5) from Ngofe Marsh confirmed that these sediment layers contain tephra. The samples have not been geochemically matched to specific eruption events.

3.3 | Regional analyses of multiple pollen records from Tonga

According to the linear model results of all four study sites, tephra falls from volcanic eruptions do not significantly explain the dynamics of littoral, mangrove, rainforest, successional/ disturbance, or wetland vegetation at different points in time, ($p > .05$, see Table 2). Meanwhile, RSL significantly explains vegetation group dynamics at Ngofe Marsh (littoral, $p < .001$, $R^2 = 0.3$; wetland, $p < .001$, $R^2 = 0.4$), Lotofoa Swamp (mangrove, $p < .01$, $R^2 = 0.4$; wetland, $p < .05$, $R^2 = 0.4$), and Finemui Swamp (littoral, $p < .01$, $R^2 = 0.03$; mangrove, $p < .001$, $R^2 = 0.7$; successional/ disturbance, $p < .01$, $R^2 = 0.3$; wetland, $p < .001$, $R^2 = 0.7$; Table 2). The model coefficients show that successional/ disturbance and littoral taxa have a negative relationship with RSL, whereas mangroves taxa have a positive relationship with RSL. Wetland taxa show mixed coefficients.

The analysis of how vegetation groups change over time shows that Ngofe Marsh's mangrove and rainforest taxa were relatively abundant between ~7000 and 4000 cal. years BP after which their abundances declined (Figures 2 and 3a). Successional/ disturbance, wetland, and littoral taxa all increased within the last ~4000 years (Figure 3a). Percentage data from Avai'o'vuna Swamp shows that littoral taxa were relatively abundant at ~5000 cal. years BP and declined in abundance subsequently. Wetland taxa increased toward the present, and rainforest, successional/ disturbance and mangrove abundances were all relatively stable (Figure 3b). For the other sites, the vegetation

TABLE 2 Temporal trends of littoral, mangrove, rainforest, successional/ disturbance, and wetland vegetation groups as revealed by linear models.

Site	Drivers of change	Littoral	Mangrove	Rainforest	Successional/ disturbance	Wetland
Ngofe Marsh ('Uta Vava'u Island, Vava'u Group)	RSL	R^2 = 0.3 ($p < .001$) Negative coefficient	($p > .05$)	($p > .05$)	($p > .05$)	R^2 = 0.4 ($p < .001$) Positive coefficient
	Tephra	($p > .05$)	($p > .05$)	($p > .05$)	($p > .05$)	($p > .05$)
Avai'o'vuna Swamp (Pangaimotu Island, Vava'u Group)	RSL	($p > .05$)	($p > .05$)	($p > .05$)	($p > .05$)	($p > .05$)
	Tephra	($p > .05$)	($p > .05$)	($p > .05$)	($p > .05$)	($p > .05$)
Lotofoa Swamp (Foa Island, Ha'apai Group)	RSL	($p > .05$)	R^2 = 0.4 ($p < .01$) Positive coefficient	($p > .05$)	($p > .05$)	R^2 = 0.4 ($p < .05$) Negative coefficient
	Tephra	($p > .05$)	($p > .05$)	($p > .05$)	($p > .05$)	($p > .05$)
Finemui Swamp (Ha'afeva Island, Ha'apai Group)	RSL	R^2 = 0.3 ($p < .01$) Negative coefficient	R^2 = 0.7 ($p < .001$) Positive coefficient	($p > .05$)	R^2 = 0.3 ($p < .01$) Negative coefficient	R^2 = 0.7 ($p < .001$) Positive coefficient
	Tephra	($p > .05$)	($p > .05$)	($p > .05$)	($p > .05$)	($p > .05$)

Note: R^2 are reported to show the strength of relationships and *p*-values indicating significance are given in parentheses. For significant results, the directions of the coefficients are given (positive or negative relationship).

groupings show that at Lotofoa Swamp, wetland taxa constituted the most dominant vegetation type at ~7000 cal. years BP, but decreased at ~3000 cal. years BP, then increased again to become the most dominant group toward the present. Mangrove taxa increased until ~3000 cal. years BP, but then began to decline. Littoral, rainforest, and successional/ disturbance taxa were somewhat stable (Figure 3c). For Finemui Swamp, mangrove taxa dominated the record until ~500 cal. years BP, after which successional/ disturbance, littoral and wetland taxa increased. Rainforest taxa remained at relatively low abundances throughout the record (Figure 3d).

4 | DISCUSSION

4.1 | Regional trends and drivers of vegetation change

Vegetation groups within the Tongan archipelago show different patterns of change throughout the Mid- and Late-Holocene (Figure 3). Our analyses suggests that RSL has been an important driver of change for littoral, mangrove, successional/ disturbance, and wetland vegetation at Ngofe Marsh, Lotofoa Swamp, and Finemui Swamp (Table 2). In contrast, volcanic eruptions have not been a driver of change for any of the vegetation groups from any of the islands included in the analysis (Table 2).

One explanation for the nonsignificant results for tephra deposition is that vegetation in Tonga might be resilient or resistant to volcanic activity. However, tephra layers deposited at Lotofoa Swamp and Finemui Swamp were relatively thick (50 and 37 cm, respectively) and might be expected to have caused vegetation changes, given that the magnitude and persistence of ecological impacts are often related to ash thickness (Dale et al., 2005). Mangroves, for example, can suffer mortality after their roots have been buried in sediments 50 cm deep (Ellison, 1999). Further research tying tephra geochemical data to known regional eruption dates and locations will bring improved information on the understanding of sources of tephra ash and distances from the sites. In addition, the temporal resolution of pollen records may present a challenge for capturing rapid vegetation changes or recoveries following volcanic eruptions. For example, the Avai'o'vuna Swamp pollen record has one pollen sample every ~440 years, Lotofoa Swamp has one sample every ~300 years, Finemui Swamp has one sample every ~200 years, and Ngofe Marsh has one sample every ~120 years, potentially limiting the identification of vegetation responses and recoveries following short-lived eruption events, which can occur on shorter timescales (see Strandberg et al., 2023). Our results, however, suggest that volcanic eruptions did not have multicentennial scale impacts on vegetation of these islands.

An additional challenge encountered was related to the classification of certain fossil pollen taxa according to vegetation groups. For example, *Cocos nucifera* and *Casuarina*, which may be considered as introduced in some parts of the South Pacific (see Fall, 2010 for discussion), may also be considered a coastal or littoral taxa (Whistler, 1992). In our analysis, *Cocos nucifera* and *Casuarina* have been included in the littoral taxa group. *Pandanus* is another example of a genus which can be placed into two vegetation types since it is both a coastal and littoral tree (Whistler, 1992) and is also somewhat fire tolerant (Prebble et al., 2005), indicating that it may be considered a disturbance or successional taxon. In our analysis, we have placed *Pandanus* in the littoral group.

Although in this study we focus on RSL and volcanic eruptions, we would like to highlight that Holocene proxy precipitation and

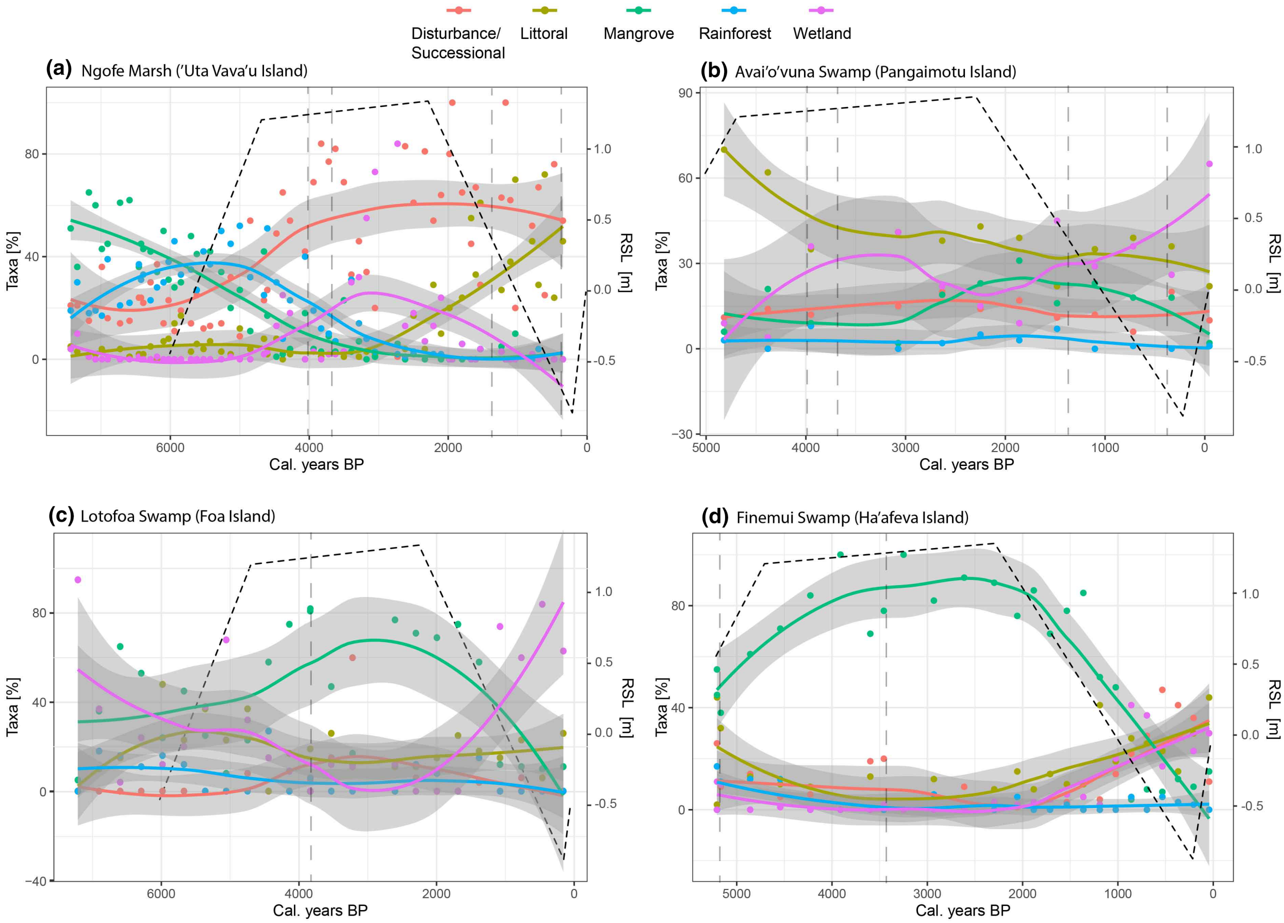

FIGURE 3 Temporal change of vegetation groups for each island using local polynomial regression fittings. The four sites are organized from north to south: (a) Ngofe Marsh ('Uta Vava'u Island), (b) Avai'o'vuna Swamp (Pangaimotu Island), (c) Lotofoa Swamp (Foa Island), and (d) Finemui Swamp (Ha'afeva Island). Trend lines indicate changes in fossil pollen percentages for successional/disturbance related taxa (pink), littoral taxa (olive green), mangrove taxa (green), rainforest taxa (blue) and wetland taxa (purple). Confidence intervals of 95% are shown in grey. The RSL curves (dashed black line) are redrawn from Fukuyo et al. (2020) for each site. Tephra layers are shown as vertical dashed lines.

temperature records from Tonga are currently absent and data linking vegetation responses to climate events are limited. Exceptions come from Efate, Vanuatu, where a decline in rainforest vegetation was interpreted as being caused by drier conditions between 3790 and 3600 cal. years BP (Combettes et al., 2015). Another study from Vanuatu shows increased vegetation turnover associated with a shift from wetter to drier conditions 1100 cal. years BP (Strandberg et al., 2023). In Fiji, a possible dry phase and change in fire regime may indicate a response to an increase in ENSO events 5000 ca. years BP (Hope et al., 2009).

The same limitations occur with datasets of human-related impacts, such as anthropogenic fires. Microcharcoal datasets, which indicate regional fires, or fire intensity, are only available from Ngofe marsh and Avai'o'vuna Swamp. For example, for Ngofe marsh, microcharcoal particles increased after ~5000 cal. years BP, prior to human arrival, which is dated 2805–2760 cal. years BP for Vava'u (Burley et al., 2015). However, fire cannot be considered a regional event since at Avai'o'vuna Swamp, located ~6 km away, microcharcoal particles were first detected between 2850–2410 cal. years BP (2620 ^{14}C years BP, Fall, 2005). There are also no tephra layers associated with the first peaks in microcharcoal ~5000 cal. years BP and pre-human fires may have been caused by lightning strikes. In addition, local fire data (i.e., macrocharcoal particles) are only available for Ngofe Marsh. These data indicate that high concentrations of macrocharcoal are only found from 2040 cal. years BP, indicating a potential association with human-related impacts (Figure 2). Fire history for Tonga is therefore far from being resolved, and this currently prevents further regional analysis. It is also still unlcear to what degree macrocharcoal fragments indicate spatial variation in burning or differences in fire intensity.

4.2 | Relative sea level and direction of vegetation changes

We found different relationships between RSL and vegetation groupings, from a nonsignificant relationship for rainforest taxa to significant relationships for littoral, mangrove, successional/disturbance, and wetlands. While the nonsignificant relationship for rainforest taxa might be explained by rainforest habitat being located on the inland portion of the islands, the explanation for the other vegetation groups is more complex. For example, wetland taxa display a complex pattern of responses to RSL change, demonstrated by both positive and negative coefficients (Table 2). When RSL was higher (5000–2000 cal. year BP), more wetland taxa were present at Finemui Swamp and Ngofe Marsh (excluding Cyperaceae for Ngofe Marsh). However, wetland taxa increased at Lotofoa Swamp when RSL started to decline ~2000 years ago. These results indicate that site-specific factors, such as local hydrology (e.g., driven by climate changes), as well as hydroseral development, may be important for the development of Tongan wetlands (Table 2). For example, RSL was at a similar level to today at Ngofe Marsh ~5500 cal. years BP but mangrove pollen was found to be present at that time but is missing from recent samples. Sediment infilling of the Ngofe Marsh basin may be the cause of this difference in vegetation.

Mangrove responses are more straightforward to interpret, for example, mangrove forests were relatively more abundant at Lotofoa Swamp and Finemui Swamp, when RSL was higher during the Mid-Late Holocene high-stand ~5000–2000 cal. years BP (Figure 3; Ellison, 1989; Fall, 2005). Two scenarios may provide possible explanations for this. The first scenario is that rising sea levels caused landward migration of mangrove taxa. The second, is that higher RSL led to increased water height and salinization of the wetlands through the permeable limestone bedrock. Since *Excoecaria agallocha* pollen (native mangrove), usually reflects local presence (Pandey & Holt, 2018), the second scenario is perhaps more plausible.

While lower RSL corresponds with increases in the littoral group at two sites (Ngofe Marsh and Finemui Swamp), higher sea levels led to the decline of the successional/disturbance taxa group at Finemui Swamp (Figure 3). During the same time period, however, there was an increase in human impacts in the region, 2805–2760 cal. years BP (Burley et al., 2015), noted by (Ellison, 1989, Fall, 2005) to coincide with a fall in sea level, and this may suggest an alternative driver, or perhaps two drivers, of change.

4.3 | A summary of 7400 years of vegetation change at Ngofe Marsh, 'Uta Vava'u Island, Vava'u group

Between 7400 and 5000 cal. years BP, Ngofe Marsh, which is currently a sedge wetland, was likely a freshwater lake surrounded by mangroves (Rhizophoraceae) and diverse primary rainforest, with Arecaceae, *Elaeocarpus* (ma'ama'alava), Sapotaceae, *Syzygium*, and *Rhus* (tavahi). After 5000 cal. BP, mangroves declined, and there was an increase in ferns, including *Microsorum*, *Stenochlaena*, possibly *S. palustris* (pasivaka), and unidentified fern taxa (monolete spores). Sedges (Cyperaceae), grasses (Poaceae), the trees *Macaranga*, *Trema*, and the tree-like-monocot *Pandanus* have dominated over the last two millennia after the transition from lake to sedge wetland, and the increasing occurrence of grass pollen indicates opening up of the landscape around Ngofe Marsh, with forest being replaced by agricultural land and settlements, as is seen today on 'Uta Vava'u.

The tephra layers (T2 ~3970 cal. years BP and T3~3670 cal. years BP in Figure 2) coincide with a 300-year period of high *Trema* pollen values. *Trema*, a native successional tree, is associated with volcanic ash falls and is classed as a successional/ disturbance taxon in our regional analysis (Flenley et al., 1999; Wallin & Martinsson-Wallin, 2010). However, our regional analysis (Table 2) did not identify tephra as a driver of change in the successional/ disturbance group.

At around 2670 cal. years BP, native secondary forest taxa *Macaranga* and *Pandanus* increased, but some other native forest taxa, many of which are considered to be primary rainforest taxa, such as *Bischofia*, *Dysoxylum*, *Elaeocarpus*, Fabaceae, *Rhus*, Sapotaceae, and *Syzygium*, declined (Figure 2). This forest decline likely reflects human arrival and its impacts. In addition, *Macaranga*, which is a secondary forest taxon common on disturbed land (Whistler & Atherton, 2015), increased after the arrival of humans at ~2670 cal. years BP (Figure 2). An increase in *Macaranga* and *Pandanus* (which can indicate disturbance, see above) after human arrival was also observed at Avai'o'vuna Swamp (Fall, 2005) and Finemui Swamp (Flenley et al., 1999). Our analysis shows that rainforest-type vegetation is not impacted by volcanic eruptions or RSL change; however, we may attribute the decline in native rainforest taxa to human impacts, such as deforestation and/ or burning after ~2670 cal. years BP. No introduced taxa, other than *Casuarina* (see Fall, 2010 for discussion), are associated with initial human arrival in this study (Ngofe Marsh), suggesting that the area in the vicinity of Ngofe Marsh was not heavily populated by people or used for taro/talo (*Colocasia esculenta*) cultivation; indeed, to the best of our knowledge to date, no archaeological findings from the colonization period have been reported in this area of southwest 'Uta Vava'u Island.

4.4 | Island size and vulnerability to relative sea level changes

Recently, islands have gained considerable focus due to concerns over their vulnerability to sea level rise (Fernández-Palacios et al., 2021). Small areas and low elevations are features generally considered to increase the vulnerability of an island to sea level rise and coastal flooding (Veron et al., 2019). The island of Ha'afeva is the smallest island included in this study (135 ha), and it is also low-lying (14 m a.s.l. maximum elevation) making it the most vulnerable to RSL change of the islands (Table S1). Our results are consistent with this description and show that the island vegetation (littoral, successional/ disturbance, mangrove, and wetlands) seems to be particularly sensitive to RSL changes (Table 2). Additionally, small islands have smaller population sizes making them more vulnerable to loosing taxa (Frankham, 2001; Keppel et al., 2014; Mueller-Dombois, 1998). On the contrary, results from the sites located on somewhat larger and higher islands, do not display such a strong association with RSL change (Table 2). It is important to highlight that Avai'o'vuna Swamp, located on Pangaimotu Island, showed no significant associations. Vegetation groups at this site appeared to be less variable than the other sites, perhaps indicating that vegetation at this wetland, or on this island is somewhat buffered from environmental changes.

5 | CONCLUSIONS

Considering projections of future sea level rise across the Pacific islands, studies like this demonstrate the complex influences on island biodiversity and specifically on coastal habitats. Our results highlight that RSL was a driver of vegetation change at three out of four of our study sites, with the smallest island (Ha'afeva) the most impacted. A better understanding of past periods of higher sea level may help to anticipate how ecosystems in Tonga are likely to react to future sea level rise.

Although results indicate the nonsignificance of tephra deposition as a driver of change on Tonga's vegetation, vegetation responses may have not been detected for several reasons. It may be, for example, that factors such as the distance of sites from the sources of eruptions served to minimize effects, though some observed tephra layers were moderately thick. Furthermore, as volcanic events are, while large, highly infrequent, there are few datapoints to test. If responses occurred but were short-lived (i.e., decades), the fairly coarse temporal resolution of these pollen datasets is not ideal. If this were the case, however, Tongan ecosystems appear in the longer term (centuries) to have been resilient in the face of regional volcanism.

AUTHOR CONTRIBUTION

NS and SN designed the study. DAS and PL did the fieldwork and NS, AC-B, IWC, and SC did laboratory work. NS, MS, and AW analyzed the data. NS and AW constructed figures. NS wrote the manuscript with substantial input from SN, ME, JCE, and WDG. All authors contributed to the writing of the manuscript.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in GitHub at https://github.com/nastrandberg/Tonga.git and Dryad https://datadryad.org/stash/share/UDpcw8lFwPp37NxN8N6rS6hbWQWHRa7la4gHoWAmRSA.

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