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The environmental impact of the Minoan eruption of Santorini (Thera): statistical analysis of palaeoecological data from Gölhisar, southwest Turkey

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Abstract: A tephra layer originating from the mid-second millennium BC (~3300 ¹⁴C yr BP) 'Minoan' eruption of Santorini (or Thera) in the Aegean has been found in lake sediments at Gölhisar in southwest Turkey. Microstratigraphic analyses of tephra shard concentration (TSC), pollen, diatoms, sponge spicules and non-siliceous microfossils in sediments from Gölhisar permit the impact of this major volcanic eruption on terrestrial and aquatic biota to be investigated quantitatively. Partial redundancy analysis and associated Monte Carlo permutation tests suggest that TSC alone cannot be shown to have had a demonstrable independent and statistically significant effect on terrestrial pollen, non-siliceous microfossil or diatom assemblages. The lack of any clear, discernible change in the terrestrial pollen composition following tephra deposition suggests that there was minimal impact on regional vegetation over decadal-to-century timescales. However, evidence that the deposition of Santorini tephra may have had an impact on the lake system comes from the combined effect of lithology and TSC (which significantly covary) that explains a significant amount of variance in the aquatic data sets. In particular, diatoms and non-siliceous algae show increases in concentration following tephra deposition, exhibiting what appear to be ±decadal response times to perturbation. These imply enhanced lake productivity due to accelerated input of silica and other nutrients following tephra dissolution.

Key words: Santorini, Thera, Minoan, volcanic impact, pollen, diatoms, redundancy analysis, variance partitioning, Monte Carlo permutation tests, late Holocene.

> 1994; Camuffo and Enzi, 1995; Sadler and Grattan, 1999). Indirect impacts occur when eruption products (especially SO_2) are ejected into the stratosphere which may produce a sulphuric

> acid aerosol that can have the capacity to interfere with the planet-

ary albedo, thereby causing short-term climatic perturbations

(Robock and Mao, 1995). When tephra shards are deposited as

layers in lakes, mires and deep-sea sediments, and are accurately

characterized, they have the potential to provide a record of

Introduction

Volcanic eruptions have the potential to cause substantial impacts on human and natural ecosystems. Direct impacts may occur due to the direct deposition of tephra and other pyroclastics, including gaseous compounds in the troposphere (Grattan and Charman,

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volcanism as well as producing excellent time-synchronous marker horizons which facilitate correlation of sites across large regions (Knox, 1993; Eastwood *et al.*, 1998b). Tephra layers also provide a unique opportunity to investigate the effect of past eruptions on biota and their environment (Lotter and Birks, 1993), and the timing of recovery of perturbated ecosystems (Barker *et al.*, 2000).

Santorini volcanic eruption: dynamics and postulated environmental effects

One of the most powerful volcanic eruptions known to have occurred during the Holocene was the mid-second millennium BC (~3300 14 C yr BP) 'Minoan' eruption of Santorini (or Thera) in the southern Aegean Sea (Figure 1A). Volcanological reconstructions suggest that the eruption of Santorini volcano commenced with a plinian phase and then went through phreatomagmatic and ignimbrite emplacement phases producing a total of around 30 km³ dense rock equivalent (DRE) of mainly rhyolitic ejecta (Pyle, 1990; Sigurdsson *et al.*, 1990; Sparks and Wilson, 1990). Previous estimates of tephra distribution derived from the investigation of deep-sea cores suggested a predominantly southeasterly dispersal plume (Watkins *et al.*, 1978; Vinci, 1985; Federman and Carey, 1980; Ninkovich and Heezen, 1965; Stanley and Sheng, 1986), but later discoveries of Santorini tephra in deep-sea cores from



Figure 1 (A) Location map of the eastern Mediterranean showing the site of Gölhisar together with sites where Santorini tephra has been discovered (figures in parentheses denotes thickness of tephra in cm). Dashed line depicts the currently accepted direction of major tephra fallout (data from Pyle, 1990; McCoy and Heiken, 2000; Momigliano, 2000). (B) Geological map of the Gölhisar catchment (modified after Senel, 1997).

the Black Sea (Guichard *et al.*, 1993) and substantial deposits in western Anatolian lake deposits (Sullivan, 1988; 1990) suggest a predominantly northeasterly axis of dispersal (McCoy and Heiken, 2000; Figure 1A). The recent detection of a 4 cm thick layer of Santorini tephra in lake deposits from Gölhisar Gölü in southwest Turkey (Roberts *et al.*, 1997) supports a northeasterly axis of tephra dispersal (Pearce *et al.*, 2002).

The possible effects that the Santorini eruption may have had on natural and cultural environments has attracted much attention since Marinatos (1939) first hypothesized that it may have caused the destruction of the Minoan civilization based on Crete. It is indisputable that the Santorini eruption impacted directly on the late Bronze Age settlement of Akrotiri on Santorini island, burying it Pompeii-style in several metres of pyroclastic deposits. However, archaeological excavations and tephrastratigraphy at the archaeological site at Mochlos on Crete have shown that the eruption occurred towards the end of the Late Minoan IA period, whereas the collapse of the Minoan civilization is relatively dated to Late Minoan IB (Soles et al., 1995). Other catastrophe theorists (e.g., Baillie, 1989; Burgess, 1989; White and Humphreys, 1994; La Moreaux, 1995) have suggested widespread cultural impacts associated with the Santorini eruption; unfortunately these hypotheses are not based on any direct cause/effect evidence. Similarly, the Santorini eruption has been implicated in many widespread environmental impacts. Several recent attempts have been made to relate inferred mid-second millennium BC climatic variations, as manifested in anomalous tree-ring growth rates and acidity peaks registered in ice cores from Greenland to the Santorini eruption. One such acidity peak recorded in the Dye 3 ice core from Greenland is dated to 1645 \pm 20 BC and equates to ~200 million tonnes of atmospheric sulphur (Hammer et al., 1987; Sigurdsson et al., 1990). The Minoan eruption of Santorini, assigned a volcanic explosivity index (VEI) of 6 by Newhall and Self (1982), was deemed the most likely candidate for correlation with this acidity peak on the basis that it was the largest known eruption for this time period. However, other large-scale eruptions encompass the same time period and make suitable candidates (Mullineaux et al., 1975; Miller and Smith, 1987; Vogel et al., 1990; Begét et al., 1992). Furthermore, a Santorini provenance for the 1645 BC acidity peak, based on geochemical analyses of ice-embedded tephra, has been questioned by Zielinski and Germani (1998).

While acidity peaks in ice cores are highly likely to have a volcanic origin, anomalous growth rings in trees will have been caused by climate perturbations which may or may not have any connection with volcanism. Narrow growth rings indicating frost damage have been found in bristlecone pines in western USA for the years 1628-26 BC (La Marche and Hirschboek, 1984), while bog oaks in western Europe display severely restricted growth for the decade commencing 1628 BC, possibly as a result of increased waterlogging (Baillie and Munro, 1988). An environmental disruption is also registered in a floating Swedish tree-ring record dated to 1635 BC ±65 years (Grudd et al., 2000). A composite floating tree-ring chronology using juniper, cedar and pine timbers from archaeological deposits in western Turkey shows a significant positive anomaly (200% of normal) at 1641 +76/-22 BC which indicates enhanced, not reduced, tree growth for a period which lasted not more than 10 years (Kuniholm et al., 1996). Kuniholm et al. (1996) correlate their tree-ring chronology with those from the USA and western Europe and, although there appears to have been some hemispherical- or global-scale climatic perturbation during the mid-seventeenth century BC, no definite cause/effect relationship between this and the Minoan eruption of Santorini can presently be demonstrated.

Aims and objectives

The present study is the first attempt to investigate the possible distal effects of the eruption of Santorini (Thera), and for this we use the lake site of Gölhisar in southwest Turkey, ~400 km ENE of Santorini volcano. The investigation adopts a statistical approach to detect the possible impacts that this major mid-second millennium BC eruption may have had on terrestrial and aquatic biota. It is conducted in direct association with a distal tephra layer firmly attributed to the Santorini (Minoan) eruption and takes place within the zone of tephra deposition in southwest Turkey as delimited by tephra isopach maps (Pyle, 1990; Sigurdsson et al., 1990; McCoy and Heiken, 2000; Pearce et al., 2002; Figure 1A). In terms of proxy data that might reflect such impacts, pollen can elucidate short-lived perturbations to terrestrial vegetation, as well as reflecting longer-term landscape and climate dynamics. Within aquatic ecosystems, diatom assemblage composition and abundance provide a sensitive index of alterations to limnological conditions, including nutrient status, pH, conductivity/salinity and light climate. However, diatoms represent only a proportion of the biomass in lake ecosystems and changes in other indicators can provide both alternative and complementary lines of evidence (e.g., Sayer et al., 1999). In addition to diatom analysis, it is possible to assess changes in other components of lake ecosystems, including aquatic macrophyte composition and abundance (aquatic pollen and other microfossil remains), algae (coenobia of Coelastrum and Pediastrum) and sponge spicules.

The sediments of the lake ecosystem at Gölhisar are well suited to assessing the regional impact of tephra deposition, as they include the distal component of the Santorini tephra layer in a continuous, replicated sequence (see Figure 2 in Eastwood et al., 1999a), thereby allowing possible cause/effect relationships to be established directly from proxy palaeoecological data. The tephra was deposited at a depth of between ~245 and 275 cm (see Eastwood et al., 1999a, Figure 2 and text, for explanation) and consists of transparent, colourless, vitric shards and pumice fragments from submicron to $>200 \,\mu$ m in size. Morphologically, the tephra consists of platey shards together with fluted, elongate-shaped pumice fragments and vesicular pumice fragments characterized by flattened spheroidal or ellipsoidal vesicles and typically rhyolitic in nature. Geochemical studies undertaken on the glass shards from the tephra deposit at Gölhisar by Eastwood et al. (1998a; 1999a) and Pearce et al. (2002) show unequivocally that the provenance of the tephra is the ~3300 ¹⁴C yr BP or mid-second millennium BC 'Minoan' eruption of Santorini or Thera. Radiocarbon age determinations on the peat underlying the tephra layer at Gölhisar (3300 ± 70 and 3225 ± 45 yr BP; Eastwood *et al.*, 1999a) support the geochemical results on a Santorini provenance for the tephra. These ¹⁴C ages do not, however, help to break the present impasse concerning an exact and much-needed calendrical date for the eruption due to the assigned errors and the nature of the calibration curve for this period (Housley *et al.*, 1999). The lake sediments at Gölhisar also contain well-preserved pollen, diatom and sponge-spicule records. We have carried out fine-interval stratigraphic investigations of these palaeoecological indicators from sediments associated with this tephra, and here test the null hypothesis that the Santorini eruption and its subsequent tephra deposition had no effect on either the terrestrial vegetation or the aquatic ecosystem at Gölhisar in southwest Turkey.

Although the evaluation of competing hypotheses is not new in palaeoecology (e.g., Flower and Battarbee, 1983), they have usually been tested through the falsification or verification of multiple working hypotheses (cf. Chamberlain, 1965) and/or are reliant on site-specific conditions (e.g., Peglar and Birks, 1993). The evaluation of multiple causal factors, though a useful approach, is hampered by the possibility of confounding effects (e.g., vegetation succession, lake ontogeny). However, with the advent of appropriate statistical techniques (ter Braak and Prentice, 1988; ter Braak and Smilauer, 1998) and associated computer-intensive randomization and permutation tests (Birks, 1998), confounding effects may be partialled out to evaluate statistically the responses of palaeoecological variables to environmental perturbations. For example, Lotter and Birks (1993), Birks and Lotter (1994) and Lotter et al. (1995) used (partial) redundancy analysis (RDA; ter Braak, 1994) to investigate the effects of the ~11 500 ¹⁴C yr BP Laacher See eruption in Germany on terrestrial and aquatic biota. Similarly, Barker et al. (2000) investigated diatom responses to tephra deposition in crater-lake sediments from Tanzania using variance partitioning and rate-of-change analysis. In the Gölhisar study a series of (partial) redundancy analyses is applied using the composition and concentration of key terrestrial and aquatic ecosystem assemblages as response variables, and with changes in Santorini tephra, changes in local depositional environment and time as predictor or explanatory (co)variables.



Figure 2 Lithology, loss-on-ignition and microfossil concentration data for the Gölhisar short core GHE.93-6 (sed = sediment).

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The study area

Gölhisar Gölü (37°8'N, 29°36'E; elevation 930 m) is a small (~4 km²), shallow (~2.5 m) lake located in the Oro-Mediterranean vegetation zone of the Lycian Taurus Mountains in southwest Turkey (Figure 1A). A substantial ancient fortified structure identified as the historic site of 'Sinda' by Hall (1994) is situated on a peninsula protruding into the lake from its northeastern shore (Figure 1B). The lake's hydrological catchment is ~88 km², and rises to an elevation of 2095 m. The catchment to lake area (z) ratio is 22:1, or 17:1 when the alluvial lowlands to the north of the lake are excluded. The modern lakewater is alkaline and oligosaline (Table 1). The slopes around the southeast of the basin consist mainly of Mesozoic limestone. Ultrabasic rocks (peridotite, serpentinite) are exposed to the east, whereas Neogene marl outcrops to the southwest and cherty limestone to the south of the lake (Figure 1b). Average annual precipitation for Gölhisar is ~600 mm, of which ~50% falls during DJF and 12% during JJA (Meteroroloji Bülteni, 1974). Present-day land use immediately surrounding the lake comprises mostly cultivated fields, while the hills and rocky outcrops are generally barren, probably largely through subrecent deforestation and overgrazing. Degraded oak scrub (Quercus coccifera) occurs on the slopes surrounding the lake with pine (Pinus brutia, P. nigra) at higher elevations.

Bottema and Woldring (1984) described the pollen stratigraphy of a ~2 m long lake marginal core from Gölhisar. The basin was reinvestigated in greater detail in 1992 and 1993 when further cores and peat sections were obtained. One of these cores (GHA: 8.13 m long) has a basal age of about 9500 ¹⁴C yr BP and records the development of Holocene woodland comprising oak, pine and juniper, followed by a period of human impact (the Beyşehir Occupation, or BO phase) which is characterized by fruiticulture (olives, manna, pistachio, walnut), cereal-growing and pastoralism (Eastwood *et al.*, 1998b; 1999b). Radiocarbon dating indicates that the BO phase at Gölhisar Gölü began at ~3160 ¹⁴C yr BP (cal. ~1400 BC) – shortly after the deposition of the Santorini tephra layer (dated to ~3300 ¹⁴C yr BP; cal. ~1613 BC) – and continued until ~1300 ¹⁴C yr BP (cal. ~AD 700) when pine became the dominant pollen type.

Diatoms are preserved in most of core GHA and comprise predominantly freshwater alkaliphilous periphytic or benthic taxa (see Figure 11 in Eastwood *et al.*, 1999b). This suggests relatively shallow but permanent waters at this lake-marginal site. The early-Holocene record includes diatoms such as *Cymbella* spp. and *Cocconeis placentula* which live attached to aquatic macrophytes. Towards 6000 ¹⁴C yr BP some taxa (e.g., *Nitzschia* spp.) are present which tolerate slightly brackish waters, and this is followed by a zone of poor diatom preservation. Above the Santorini tephra layer (STL) diatoms are better preserved and species assemblages are less variable stratigraphically, being dominated by species of small *Fragilaria*. The time interval studied was deliberately selected after analysis of the long sequences, so as to be 'nested' within millennialscale environmental changes, and with a sampling interval fine enough to permit annual-decadal responses to tephra deposition to be evaluated. The mid-second millennium BC eruption of Santorini (Thera) occurred prior to major human-induced deforestation in the Gölhisar catchment (Eastwood *et al.*, 1999b), which means that any volcanic impacts would have been registered on what was a largely natural landscape. The short duration of the interval under study also implies that variables which are significant on a Holocene timescale (e.g., lake ontogeny, forest succession) are unlikely to have been important over short times and their influence can appropriately be 'partialled out' statistically.

Sampling, analytical and statistical methods

The GHE series of sediment cores (see Figure 2 in Eastwood et al., 1999a), obtained specifically to provide material with which to test the hypotheses advanced in this study, were retrieved using a 30 cm long, 3 cm diameter Dachnowsky corer. Cores were extruded in the field, wrapped in clingfilm, placed in labelled sections of PVC guttering cut lengthways, and then wrapped in heavy-duty plastic sleeving. Upon return to the laboratory the cores were stored at ~4°C. The sediments were described in the field and in the laboratory using a modified version of the Troels-Smith (1955) scheme as proposed by Aaby and Berglund (1986). The upper 16.5 cm of short core GHE.93-6, taken at the southeastern lake margin, starting at a depth of 240 cm, was selected for detailed investigation. Unlike lake-centre cores from Gölhisar, where bioturbation and other mixing processes have led to vertical diffusion and blurring of the Santorini tephra layer in a predominantly unconsolidated lake-mud matrix, the 4 cm thick layer of tephra at the GHE core site appears to have been deposited directly on a peat surface and is well preserved as a distinct horizon, and is thus suitable for testing the palaeoecological hypotheses outlined in this paper.

The organic matter and carbonate contents of the sediments (Figure 2) have been estimated using loss-on-ignition (Dean, 1974). Samples for pollen (1 cm^3) and diatoms were taken every 0.5 cm above the tephra layer and every 1 cm below it. Pollen extraction follows the standard procedures of Faegri and Iversen (1989). Exotic Lycopodium tablets of a known concentration were added in order to estimate pollen concentrations (Stockmarr, 1971). Pollen grains and other non-siliceous microfossils were counted using a Nikon Labophot-2 microscope until a land-pollen sum of 350 grains was reached (except in the STL) with critical identifications being conducted under oil immersion at $\times 1000$, together with phase-contrast microscopy. Aquatic pollen and non-siliceous microfossils are expressed as a percentage of the total

	Table 1	Water-quality	data for	Gölhisar	Gölü
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	рН Сс (µ	Cond.	Data in molar equivalents (meq 1 ⁻¹)					Anion sum	Cation sum		
		(#Sem)	Mg	Ca	Na	K	Cl	SO₄	Carbonate		
July 1992*	8.95	1350-1500	nd	nd	nd	nd	nd	nd	nd	nd	nd
August 1996	8.3	920	8.58	1.69	1.30	0.09	0.82	1.66	7.01	9.46	11.66
April 1997	9.0	660	8.38	1.66	0.91	0.07	0.76	1.25	6.41	8.42	11.03
September 1999	8.1	765	nd	nd	nd	nd	nd	nd	nd	nd	nd
July 2000	8.4	697	nd	nd	nd	nd	nd	nd	nd	nd	nd
July 2001	8.0	867	nd	nd	nd	nd	nd	nd	nd	nd	nd

*Lake edge sample.

nd = not determined.

number of palynomorphs. Generally, pollen preservation is good, but the Pinaceae undiff. category includes grains that could not confidently be assigned to a higher taxonomic resolution and largely comprises grains that are degraded and crumpled. Fossil diatom samples were prepared using standard techniques (Battarbee, 1986) and counted in transects at $\times 1000$ magnification with a Zeiss Axioscope compound microscope equipped with differential interference contrast optics, and identified by reference to Krammer and Lange-Bertalot (1986, 1988, 1991) and other taxonomic floras. Diatom and sponge-spicule concentrations were calculated using a known area of coverslip counted and a known proportion of sample added to the coverslip. Tephra-shard concentration (TSC; Figure 2) was quantified by contact with two preselected microscope graticule points in 200 fields of view on the diatom slides along previously selected regularly spaced transects using the point count method (Clark, 1982).

Local pollen and diatom assemblage-zone boundaries were delimited on the basis of stratigraphically constrained incremental sum-of-squares cluster analyses (CONISS; Grimm, 1987) using a square-root transformation and chord-distance dissimilarity measure for the pollen and diatom types that occur at greater than 2% abundance; different palaeoecological variables (pollen, diatoms, etc.) were each zoned separately. Summary pollen and diatom diagrams were constructed using Tilia and Tilia-graph (Grimm, 1991) and show the pollen and algal types and diatoms used in the numerical analyses, while uncommon diatom species are grouped at genus level in the diagram. Numerical analyses conducted on relative abundance data included all taxa which had a representation of $\geq 1\%$ in the data sets examined.

Detrended canonical correspondence analysis (DCCA), with detrending by segments and non-linear rescaling with depth as the sole predictor variable, was used to assess the gradient length of variation in the stratigraphical data. This technique provides a measure of the compositional turnover of the data sets in relation to depth (Hill and Gauch, 1980; ter Braak and Prentice, 1988). Gradient length is fundamental to the choice of ordination technique because, over short gradients, taxa respond in a linear fashion, while over longer gradients taxa rise and fall in a unimodal manner (ter Braak, 1994; ter Braak and Prentice, 1988). All gradients in the data were short (<1.9 standard deviations) and therefore RDA, the constrained form of linear principal components analysis (PCA) ordination (ter Braak and Prentice, 1988), was used. RDA enables the effect of one or more environmental forcings on multivariate data sets to be modelled and evaluated statistically (ter Braak, 1994). Through the use of Monte Carlo permutation tests, RDA can assess whether biotic shifts associated with (palaeo)environmental phenomena (such as tephra deposition) are no more likely than would be expected by chance. Furthermore (where relevant data exist) the influence of confounding variables (termed 'covariables') can be allowed for and 'partialled out' (ter Braak, 1994).

Relative abundance data for pollen and diatom assemblages were square-root transformed, while total concentration data for pollen, diatom and sponge spicules were \log_{10} transformed prior to numerical analysis. The explanatory variables used for the RDA were depth, lithology and tephra shard concentration (TSC; Table 2).

The explanatory variable 'depth' was used here as a surrogate for time. Variance explained by depth may therefore be associated with long-term forcing mechanisms such as unidirectional climate change, soil maturation and lake ontogeny.

The variable 'lithology' included percentage organic, carbonate and minerogenic matter together with four visible sediment types (marl, clay, tephra, peat; Figure 2) each coded (0 or 1) as a separate dummy variable (cf. ter Braak, 1990a). Sediment type (lithology) is reflective of the environment in which microfossils were deposited (e.g., lake level, anoxia). Lithology is a potentially Table 2 Explanatory variables and covariables used in RDA and the rationale for their selection

(Co)variable	Factors attributable to the (co)variable
Lithology	Limnological conditions, depositional environments, changing taphonomic conditions
Depth	Unidirectional climate change, soil maturation and lake ontogeny
Tephra shard concentration (TSC)	Santorini tephra effects

important explanatory variable for the aquatic ecosystem data, as changes in lake environment may affect primary productivity and species composition. Sediment lithology may also reflect catchment landscape conditions. However, changes in lithology over the short timescale analysed in this record are unlikely to reflect processes affecting the composition of terrestrial vegetation not accounted for by the variable depth. Lithology was therefore not used as an explanatory variable for the terrestrial pollen percentage data as catchment vegetation relative composition should be unrelated to lake sedimentary facies. Lithology was used, however, as a covariable for all data sets, including pollen percentage data, in order to partial out the effect of depositional environment on microfossil taphonomy.

TSC is likely to be more representative of the effect of the Santorini tephra on ecosystems than a simple exponential decay function of shard abundance (cf. Lotter and Birks, 1993). The use of concentration values enables variation in the influence of the Santorini tephra layer (and therefore its effect) to be assessed more accurately.

In order to test the null hypothesis that the Santorini eruption had no effect on ecosystems at Gölhisar, the statistical significance of the numerical relationship between the biological variables and TSC was assessed using restricted Monte Carlo permutation tests of RDA axes. In this analysis, TSC was the only explanatory variable and the variance in the biological data explained by depth and/or lithology (representative of a range of other factors; Table 2) was partialled out (i.e., not attributed to the Santorini eruption), because the (co)variance associated with changes in depth and lithology need not be related to the deposition of the Santorini tephra.

The evaluation of the significance of TSC with the variation associated with lithological changes partialled out (using lithology as a covariable) is a strict test of the effect of the eruption's impact, as many lithological variables covary with TSC. For example, TSC and % mineral residue are significantly correlated $(r^2 = 0.37, p = 0.003)$. Furthermore, aquatic biota may contribute to changes in lithology, rather than be affected by them. Monte Carlo permutation tests of the significance of the explanatory variables involved 199 restricted permutations for time-series (ter Braak, 1990b; ter Braak and Smilauer, 1998), appropriate to stratigraphical data (Birks, 1998). The significance of RDA axis 1 was tested for each single explanatory variable, while an overall significance test was used where more than one explanatory variable was present. The RDA procedure used does not consider any significant lags in ecosystem response to TSC variance. Using this technique, ecosystem response is assumed to be synchronous over the time period represented by a single sample. For partial RDA, restricted permutations under the full model (ter Braak and Smilauer, 1998) were used.

In addition to evaluating the independent effect of the Santorini eruption, we tested several null hypotheses regarding the combined effect on the range of biological responses of TSC and changes in depth (all indicators) and the combined effect of TSC

Explanatory Covariable(s) variable(s)		Terrestrial pollen		Aquatic palynomorphs	Aquatic pollen	Sponge spicules	Diatom	
		%	Conc.	%	Conc.	Conc.	%	Conc.
All	depth	0.005**	0.005**	0.005**	0.005**	0.005*	0.005*	0.005*
TSC		0.005**	na	na	na	na	na	na
TSC	depth + lithology	0.20ns	0.03*	0.06ns	0.06ns	0.10ns	0.33ns	0.88ns
TSC + depth	lithology	0.005**	0.04*	0.005**	0.25ns	0.04*	0.12ns	0.69ns
TSC + lithology	depth	na	0.005**	0.005**	0.03*	0.005*	0.005*	0.01*

Table 3 Significance levels of relationships between biostratigraphical data sets from Gölhisar, with different explanatory variables and covariables (see methods section). Significance levels are established using restricted Monte Carlo permutation tests (n = 199)

TSC = tephra shard concentration.

% = relative abundance data.

Conc. = concentration.

** = significant at p < 0.01.

* = significant at 0.01 .

ns = not significant.

na = not analysed.

and changes in sediment lithology (all indicators except terrestrial pollen composition). In each of these analyses, the variance associated with lithology and depth, respectively, were partialled out as covariables to separate their influence. The variance in the seven different palaeoecological data sets was partitioned following the approach of Borcard *et al.* (1992) using a series of (partial) RDA. The models were designed to estimate the variance in the response data sets that is explained by all predictor variables, explained by TSC independent of time and sediment lithology, explained by TSC and time independent of sediment lithology, explained by TSC and sediment lithology independent of time, and unexplained variance (Table 4).

All ordination analyses were made with the program CANOCO version 3.12 (ter Braak, 1990a; 1990b) and were re-run with CANOCO version 3.12a with strict convergence criteria.

Results

Lithostratigraphy and time duration

The upper 16.5 cm of short core GHE.93-6 comprises four lithological units (Figure 2). The lowest part of unit GE-1 (256.5-252.5 cm) is composed of black humified peat (up to 70% organic matter; Figure 2), with trace amounts of tephra shards. The slight decrease in percentage organic matter during the upper part of this unit (252.5-250.5 cm) corresponds to higher concentrations of tephra (and is labelled separately on Figure 2 as 'peat and tephra'). Unit GE-2 (249-245 cm) is comprised predominantly of tephra as highlighted by the marked increase in TSC and mineral residue (~90%). In GE-2, terrestrial pollen data exhibit a marked decrease in concentration. For the purpose of clarity, the sediments of lithological unit GE-2 are hereafter referred to as the Santorini tephra layer (STL). The apparent vertical displacement of tephra shards is a phenomenon that is not unique to the deposits at Gölhisar and has previously been reported in peat deposits and lake sediments from Scandinavia, Faroe Islands, Iceland, Northern Ireland and Scotland (Persson, 1971; Pilcher and Hall, 1992; Thompson et al., 1986; Dugmore et al., 1995; Charman et al., 1995). Unit GE-3 (245-243 cm) is composed of organic-rich siltclay with a marked decrease in TSC, while lithological unit GE-4 (243-240.5 cm) is made up of calcareous silt-clay (~10% carbonate) corresponding to a considerable increase in diatom concentrations and relatively low TSC. These visible lithological units correspond closely to quantitative analyses of sediment composition, with some minor differences at unit boundaries (e.g., measured TSC stays high in the basal sample from unit GE-3).

In the absence of annually laminated sediments, it is not possible to provide a precise estimate of the time period covered by

Table 4 Proportion of Gölhisar biostratigraphic data set variance explained by different sets of external factors (see methods section). Explanatory variables used for terrestrial pollen percentage data were TSC + depth only; for all other data sets the models used were TSC + depth + lithology. Lithology was used as a covariable with all data sets. Entries shown in parentheses have a p-value of >0.05 (Table 3) and are considered not significant

Source of variance	Explanation	Terrestrial pollen		Aquatic palynomorphs	Aquatic pollen	Sponge spicules	Diatom	
		%	Conc.	%	Conc.	Conc.	%	Conc
Temporal and lithological change and Santorini effects	All	31.3	73.0	82.7	55.8	88.0	65.0	84.8
Santorini effects independent of time and sediment change	TSC-D-L	(9.0)	26.2	(10.6)	(8.0)	(43.5)	(7.3)	(0.8)
Santorini and time effects independent of sediment change	TSC + D-L	20.8	38.2	18.5	(12.9)	60.9	(15.8)	(7.5)
Santorini and sediment change effects independent of time	TSC + L-D	19.5	72.3	70.5	52.3	87.7	48.9	58.2
Unexplained variance		68.7	27.0	17.3	44.2	12.0	35.0	11.2

TSC: tephra shard concentration.

D: depth.

L: lithology. Conc: = concentration. short core GHE.93-6. However, a broad time envelope can be provided by the ¹⁴C dated age-depth scale which exists for the long Holocene core GHA, taken from the same sampling site (Eastwood *et al.*, 1999b). Overall sediment-accumulation rates for this core range between 0.4 and 0.8 mm yr⁻¹, except for a short phase of increased sedimentation soon after the onset of the BO phase of forest clearance. In addition, for short core GHE.93-6, the tephra needs to be removed from sedimentation-rate calculations, and on this basis the 16.5 cm profile of GHE is estimated to cover a timespan of between 120 and 250 years.

Terrestrial pollen

Generally, the terrestrial pollen percentage data (Figure 3) do not show any significant changes. There is very little overall change in AP values before (~85%-95%) or after (~92-96%) the deposition of the STL. Although AP values attain ~96% before the deposition of the STL, this is in just one pollen spectrum. Of the main AP types, Quercus and Cedrus show only slight increases (attaining values of ~12% and ~8%, respectively), while Pinus has a slight decrease in the samples containing the STL. Degraded and broken grains increase by ~5% and ~10%, respectively, after the deposition of the STL (Eastwood, 1997) which may be a function of degradation as a result of increased runoff after deposition of the tephra layer. Of the non-arboreal pollen (NAP) types, Gramineae shows a slight increase (to ~20%) in the samples containing elevated TSC and then declines to its lowest values following tephra deposition (~5%). In short, percentage pollen data do not suggest any significant effect on terrestrial vegetation. A ~14% decrease in Pinus pollen, which is a notoriously high pollen producer, and which constitutes most of the AP, is not considered to be representative of any significant ecological changes. In addition, firm ecological interpretations are further hampered due to the limitations imposed on palynological data to record accurately ecological plant associations (Bottema, 1982), as well as limitations imposed due to dispersal, representation and preservation.

RDA shows that all relevant explanatory variables (in this case, TSC and depth; Tables 3 and 4) in combination explain a statistically significant (p = 0.005) amount of variance (31.3%) in the relative abundance terrestrial pollen data. However, analysis of the STL effects, with the variance associated with depth and lithology partialled out, shows that TSC independently explains a much smaller and statistically insignificant amount (p = 0.20) of the variance (9.0%). TSC with only the unidirectional variance associated with depth partialled out, on the other hand, explains a significant (p = 0.005) amount of the variance (19.5%) in the pollen percentage data.

A much greater amount of variance in the total terrestrial pollen concentration (73%, p = 0.005) is explained using all the explanatory variables in combination (TSC, depth and lithology) than in the relative abundance data. In contrast to the relative abundance data, TSC independently (i.e., with the effects of depth and lithology partialled out) explains a statistically significant (p = 0.03) amount of variance in terrestrial pollen concentration (26.2%). A significant (p = 0.005) amount of variance in terrestrial pollen concentration is explained by TSC and lithology, with depth partialled out as a covariable (72.3%).

Aquatic palynomorphs and sponge spicules

Of the aquatic palynomorphs (i.e., aquatic pollen + aquatic nonsiliceous microfossils; Figure 4), low percentages of total aquatic pollen (\leq 5%) hinder any firm palaeoecological inferences. However, Cyperaceae and non-siliceous palynomorphs (typology after van Geel *et al.*, 1989), Type 610 and Sigmopollis (Type 128B) record increases in samples in and above the STL (zones A-3 to A-5). *Ceratophyllum* leaf spines have relatively high percentage values in the basal zone (A-1), and also a minor increase in samples above the STL (zone A-4), while coenobia of *Pediastrum* and, to a lesser extent, *Coelastrum* show marked increases above the STL during zone A-5.

Aquatic palynomorph assemblages respond significantly (p = 0.005) to the combined effects of TSC, depth and lithology (variance explained: 82.7%). However, the independent influence of TSC (with depth and lithology partialled out) on aquatic palynomorph variance (10.6%) is not statistically significant (p = 0.06). Variance explained by TSC and lithology combined, with the effects of depth partialled out, is statistically significant (70.5% p = 0.005).

The combined explanatory variables explain only around half the variance in aquatic pollen concentration (55.8%), and TSC as an independent variable does not account for a significant (p = 0.06) amount of variance (8.0%). In accordance with all other data sets evaluated, changes in TSC and lithology explain a statistically significant amount of variance in the aquatic pollen concentration, even when the effects of depth are removed as a covariable (52.3% p = 0.03).

A large and significant (p = 0.005) amount of sponge-spicule concentration variance (88%) is explained by TSC, depth and lithology combined. Interestingly, the proportion of sponge-spicule variation explained by TSC and lithology with the effect of depth partialled out (87.7%) is almost the same as that explained by all variables (Table 3). Despite explaining approximately two-fifths of the variance in spicule concentration, the effect of TSC alone is not statistically significant (p = 0.10). TSC and depth explain a significant portion of variance in sponge spicules (p = 0.04; 60.9% variance explained) with lithology included as a covariable.

Diatoms

The diatom record for GHE.93-6 is dominated by small *Fragilaria* taxa (F. brevistriata, F. pinnata and F. construens) which, as a group, increase in abundance towards the top of the core (Figure 5). Within these, F. brevistriata and F. construens increase towards the top of the sequence, with F. pinnata being most abundant in the middle of the sequence. Apart from the increased representation of Nitzschia inconspicua in zone D-5 and the virtual elimination of Epithemia adnata from the record above D-2, there are few other unidirectional shifts in diatom species composition.

Planktonic Cyclostephanos dubius and Aulacoseira granulata, along with the littoral Amphora pediculus, have bimodal relative abundance curves; C. dubius is common in zones D-1 and D-3 while A. pediculus is well represented in D-2 and D-4. For much of the record the representation of C. dubius and Cyclotella ocellata is broadly similar; however, C. ocellata (15.2%) is considerably more abundant in zones D-4 and D-5 than Cyclostephanos dubius (max 6.7%, mean 2%). These shifts in diatom assemblage composition mirror rather closely the core lithological units. Overall, however, the most notable feature of the diatom record is the marked increase in diatom concentration above the STL, especially in zone D-5 (Figure 2).

TSC, depth and lithology in combination explain a somewhat lower proportion of variation (65%) of the diatom compositional data than for most other aquatic indicators; however, this relationship is still significant (p = 0.005; Tables 3 and 4). When the effects of depth and lithology are partialled out, a low (7.3%) and a statistically non-significant (p = 0.33) amount of the diatom variance is explained by TSC. However, TSC and lithology with depth as a covariable explain a significant (p = 0.005) proportion of the variance in the diatom data (48.9%). TSC and depth, with lithology as a covariable, are not significant (p = 0.12) explanatory variables for the diatom variance (15.8%).

Similar results to the species composition data were derived from RDA of the diatom concentrations. Only combinations of all the variables, or of TSC + lithology with depth partialled out, at Universiteisbiblicetet i on December 12, 2007.

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explained significant (p = 0.005, p = 0.01, respectively) amounts of the variance in the diatom concentrations (84.8%, 58.2%, respectively; Table 4).

Discussion

The main potential impacts of volcanic eruptions on terrestrial biota include physical damage to plants by tephra or ashfall, the presence of volatile acids in the atmosphere (direct impacts), and regional or global climate perturbation (indirect impact). The direct effects of volcanic eruptions usually have the greatest impacts in areas proximal to the volcanic eruption, although there are exceptions and these sometimes involve the deposition of acidic aerosols (Grattan and Charman, 1994; Sadler and Grattan, 1999). Palynological investigations on the direct impacts of volcanic eruptions by Wilmshurst and McGlone (1996) in New Zealand showed that there was significant damage to proximal forests following the 1850 BP Taupo eruption but only minor damage in distal areas, with forest recovery in proximal areas being completed within ~200 ¹⁴C years. Modern studies on volcanic impacts caused by the 1980 Mount St Helens eruption (Mack, 1981) report that damage to vegetation outside the actual blast zone was only slight and was related mainly to plant morphology. Tephracoating of trees was largely washed off after the first rainfall, while prostrate herbs or those with clasping leaves suffered most. Plants with long slender leaves (e.g., grasses) were hardly affected, presumably due to their ability to shed quickly any deposited tephra (Mack, 1981). The Gölhisar catchment (~400 km ENE of Santorini volcano) appears to have received a maximum of ~4 cm of distal tephra fallout. Potentially, this thickness of tephra might have been enough to cause some physical damage to low-lying herbs similar to those caused by the Mount St Helens eruption as reported by Mack (1981). Such herbs are presumably more strongly affected than tall and robust plants. This might explain the slight increase in Gramineae (and possibly Cyperaceae) pollen values as recorded at Gölhisar during and after the STL. A similar increase in Gramineae and Cyperaceae was also recorded by Lotter and Birks (1993), Birks and Lotter (1994) and Lotter et al. (1995) in their investigations on the palaeoecological effects of the Late-glacial Laacher See eruption.

Research into twentieth-century volcanically induced climatic perturbations suggests that temperature lowering occurs in the range 0.3-0.5°C and lasts for a period of 3-4 years (Mass and Portman, 1989; Robock and Mao, 1995) but the relationship between volcanic eruptions and climate fluctuations is complex (Sadler and Grattan, 1999). Kuniholm et al. (1996) have suggested that a series of anomalously wide tree-rings recorded in the Porsuk tree-ring sequence from south-central Turkey can be correlated with the Minoan eruption of Santorini. In climatic terms this would indicate cooler summers, higher precipitation and/or increased cloudiness resulting in enhanced tree growth, rather than the reduced tree growth inferred from Irish bog oaks and Californian pines at this time (Baillie and Munro, 1988; La Marche and Hirschboek, 1984). There is no other significant anomaly in the Porsuk series, positive or negative, during the first half of the second millennium BC. If, as seems feasible, this dendrological anomaly represents the climatic legacy of the Santorini eruption, the perturbation lasted only for 6-7 years based on tree-ring counts. An event of such short duration will be barely detectable in most lake or peat stratigraphies, except when annual laminations are present. Even with fine-interval sampling of lakesediment cores, subdecadal climatic change is normally likely to be represented by only a few individual spectra.

Our analyses indicate that no major change can be discerned in terrestrial pollen assemblages from Gölhisar, and hence in the surrounding terrestrial vegetation, following tephra deposition. Furthermore, even when time and STL-related effects are included in our analyses, more than two-thirds of the stratigraphic variance in terrestrial pollen composition remains unexplained (Table 4). This rules out any significant direct impacts of the Santorini tephra on regional vegetation over the timescales considered here. Indirect impacts related to any subdecadal climatic perturbation are harder to evaluate in the absence of a high-resolution chronostratigraphy. In contrast to the lack of change in pollen composition, total pollen concentration shows a clear decline during the STL, and is the only palaeoecological indicator analysed that shows a statistically significant synchronous response to TSC. We infer that the decline in pollen concentration during the STL is likely to be a dilution effect during a period of accelerated sediment accumulation, associated with the fallout and/or inwash of tephra. As such, the statistical relationship between total land pollen concentration and TSC is unlikely to have any real environmental significance.

In terms of the response of the aquatic ecosystem, some of the main potential impacts of the volcanic eruption are related to increased nutrient input, from chemical weathering of tephra or changes in lake physical condition such as sealing the sedimentwater interface or burial of lake-marginal plant communities. Sealing of the lake bed by deposition of a substantial thickness of tephra can prevent release of phosphorus into the water-column from the uppermost sediments. This, in turn, can alter the Si:P ratio of the lakewaters, favouring diatom genera such as Synedra over Aulacoseira (Barker et al., 2000). However, shallow-water conditions would argue against this being a significant contributory factor at the core site analysed here. At Gölhisar, there are marked changes in both composition and concentration of diatoms during the time period represented by the core sequence. Concentrations are low in the period before the main tephra deposition, although slightly elevated diatom concentrations in samples from 251-252 cm (Figure 2) are associated with increased TSC during zone D-2 (Figures 2 and 5). This minor increase in diatom concentration may represent initial fertilization effects by bioavailable nutrients deposited directly onto the lake surface. A possible mechanism for this would be the almost immediate dissolution of the submicron size fraction of the tephra (e.g., $<2 \mu$ m) as it filters down through the water-column (personal communication, J.A.Westgate, University of Toronto), but more work is needed to substantiate this. Interestingly, despite the deposition of the Sirich Santorini tephra (Eastwood et al., 1999a), diatom concentrations show no significant direct correlation with TSC and depth, if the effects of lithology are partialled out. Low diatom concentrations in the Si-rich environment of the STL may have resulted from tephra particles inducing light limitation, particularly given the non-planktonic habitat of many taxa in the record, but that may also be a dilution effect, as with terrestrial pollen. Cyclostephanos dubius has some of its highest abundance within the main tephra peak itself and, along with a peak in Cyclotella ocellata, contributes to a high proportion of planktonic taxa being associated with the maximum TSC values. High proportions of planktonic taxa may result from abiotic shading of non-planktonic taxa such as Epithemia adnata.

In contrast, diatom concentrations increase markedly above the STL towards the top of the short core. A similar diatom increase following tephra deposition has been recorded in lake-sediment records from other parts of the world, particularly in systems which are normally silica-deficient (Abella, 1988; Hickman and Reasoner, 1994). Unpublished modern water data for Gölhisar Gölü indicate fairly high values of silica (3.81 mg l⁻¹) which suggest that silica is not limiting in the modern system (Jane Reed, written communication, August, 2001). However, it is unlikely that silica or other nutrients in the modern lake were the same as those prior to major human catchment disturbance c. 3200 years ago, shortly after the deposition of the STL. Diatom concensities biblicket in December 12, 2007

trations in the upper part of the GHE.93-6 are by no means the highest in the Holocene history of Gölhisar Gölü (Roberts *et al.*, 1997; Eastwood *et al.*, 1999b); however, they coincide with increases in the percentage carbonate composition in the core. This may be because increased algal photosynthetic activity led to seasonal changes in lakewater pH and calcite precipitation.

One of the main apparent 'beneficiaries' in the period following tephra deposition at Gölhisar Göll were small, chain-forming *Fragilaria* species. These are often pioneer taxa (Haworth, 1976) and have also been noted to increase their representation with catchment disturbance in lake systems (e.g., Barker *et al.*, 1994). While small *Fragilaria* taxa are important in Gölhisar assemblages below the STL in the longer Holocene record (Eastwood *et al.*, 1999b), they appear to have obtained a competitive advantage in the lake after deposition of the Santorini tephra.

Percentage and concentration values of the aquatic alga *Pediastrum* increase from trace values before the STL to high values after it. There is also a less sustained increase in the value of Type 610 (typology after van Geel, written communication) immediately following deposition of the tephra. These and other nonsiliceous microfossils increase again higher up the core sequence during the BO clearance phase, associated with inwash of nutrients caused by human-induced catchment soil erosion (Eastwood *et al.*, 1998b; 1999b).

None of the aquatic ecosystem indicators analysed shows a statistically significant, synchronous response to TSC when the effects of other variables (depth and lithology) are partialled out. In part, this may be a result of using lithology as a covariable. This interpretation is supported by the significant values (p = 0.03 - 0.005) attained with RDA for all aquatic indicators analysed, when TSC and lithology are combined as explanatory variables, with depth effects partialled out (Table 3).

In general, increased concentrations of aquatic organisms (diatoms, Pediastrum and sponge spicules) occur above maximum TSC. The abundances of these microfossils, which are higher in the 240.5-244.25 cm samples than in any part of core GHE.93-6, are indicative of enhanced lake productivity. These organisms may have responded to increased nutrient loading due to inwash (as indicated by higher post-Santorini tephra proportions of mineral residue) or diagenetic alteration of tephra shards. It appears that STL deposition may have caused fertilization of Gölhisar Gölü, either directly (with nutrients being deposited onto the lake itself) and/or indirectly via mechanisms such as delivery of tephra-derived nutrients from the catchment. Increased silica availability may have been one reason for the increase in diatoms and sponge spicules post-STL, but other nutrients and/or competitive advantage resulting from, for example, shading must also have been involved to explain the synchronous changes in nonsiliceous algae.

The response of aquatic communities to atmospheric deposition of tephra or acids will depend on the relative strength of the lakecatchment buffering capacity as well as the amount and type of deposition. In contrast, for example, to lakes in Germany's Black Forest region (Lotter and Birks, 1993), Gölhisar Gölü appears to be a well-buffered system (Table 1), with much of the catchment comprising calcareous rocks (Figure 1B). Increases in nonsiliceous algae suggest it is unlikely that a 'cap' of tephra halted P release from the sediments, as suggested for other systems (Abella, 1988; Barker *et al.*, 2000).

In the absence of a reliable high-resolution chronology for short core GHE.93-6, it is difficult to assess the response time of the aquatic ecosystem to tephra impact. Below the STL, the time interval between samples is likely to be decadal (estimated at 12.5 to 25 yr⁻¹ between 1 cm interval samples). We are unable to assess the extent to which the tephra layer at site GHE represents primary ash deposition, and how far it represents secondary inwash of tephra from the catchment. However, the sharp diminution in total land-pollen concentration, and corresponding rise in TSC, suggests that the STL represents, at most, a few years' accumulation. On this basis, biological proxies within the STL would reflect responses on subannual to annual timescales. Above the tephra layer, biological responses will be annual to decadal (estimated at 4 to 12 yr⁻¹ between 0.5 cm interval samples). Thus, the observed increase in diatom concentration above the STL is likely to have involved a response time of at least a decade.

Conclusions

In this study we have investigated the impact of the \sim 3300 ¹⁴C yr BP or mid-second millennium BC 'Minoan' eruption of Santorini or Thera on terrestrial and aquatic biota via microstratigraphic analysis of tephra-shard concentrations (TSC), pollen, diatoms, sponge spicules and non-siliceous microfossils in lake sediments from Gölhisar Gölü in southwest Turkey. From the results of partial redundancy analysis and associated Monte Carlo permutation tests, the independent effect of the Santorini eruption (TSC with depth and lithology partialled out as covariables) can be shown to be statistically significant only for changes in total terrestrial pollen concentration. However, those changes in pollen concentration are likely to be due mainly to dilution effects during a period of greatly increased sediment accumulation as a consequence of tephra input, rather than as a result of suppressed pollen production. No statistically significant ecological impact of tephra upon catchment vegetation is discernible from changes in the composition of terrestrial pollen spectra prior to and after tephra deposition. Indeed, terrestrial pollen composition has the highest proportion of unexplained variance (68.7%) of any biological dataset evaluated in this study.

For aquatic data sets such as the concentration and taxonomic composition of diatoms, aquatic palynomorphs and sponge spicules, the tephra has been shown to have had no statistically significant, independent, immediate effect, when the effects of time (depth) and depositional environment (lithology) are partialled out. Notwithstanding this, it is evident that aquatic indicators, and in particular total diatom and Pediastrum concentration, changed markedly following tephra deposition. Changes in sediment lithology, including the presence of the tephra as a distinct lithological unit, serve to confound any relationship between aquatic indicators and TSC. It is therefore not possible to isolate completely the effect of tephra deposition from changes in lithology on the Gölhisar aquatic ecosystem. On the other hand, together the two indicators (tephra + lithology) explain between 48.9% and 87.7% of the variance in the different aquatic elements considered here, and suggest a much stronger link between tephra deposition and changes in lake biota than between tephra and changes in the terrestrial flora.

This study has highlighted some of the difficulties in confirming or falsifying the distal environmental impact of explosive volcanism in the palaeoecological record. Stratigraphically, most lakesediment records lack the chronological resolution necessary to test the impact of short-term post-eruptive perturbations in climate, such as the subdecadal climatic excursion suggested from anomalously wide growth rings in the Porsuk dendrochronological sequence (Kuniholm et al., 1996). Numerically, it can be difficult to take account of any lagged ecological responses and to separate predictor variables which covary, such as TSC and lithology. The mid-second millennium BC (~3300 ¹⁴C yr BP) 'Minoan' eruption of Santorini (or Thera) was one of the largest volcanic eruptions to have occurred during the Holocene and this study represents the first rigorous investigation to ascertain the environmental effects of this eruption. Our results from Gölhisar suggest that the physical and atmospheric effects of the Santorini eruption had, at most, a modest impact on distal terrestrial and aquatic ecosystems,

but that it may have had significant local fertilization effects associated with the input or release of biologically limiting nutrients. This conclusion is contrary to the deleterious environmental effects suggested by White and Humphreys (1994) or La Moreaux (1995) and now needs to be tested at other lake sites in the eastern Mediterranean.

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