Taxonomic and functional plant diversity of the Santorini-Christiana island group (Aegean Sea, Greece)

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Abstract: This is the first attempt to analyse vascular plant diversity patterns regarding the seven vegetated islands of the Santorini archipelago (Aegean Sea, Greece) as a whole. Hitherto unpublished floristic records, combined with critical use of taxonomic and chorological information from previous and most recent literature, resulted in a total of 696 infrageneric taxa (species and subspecies) occurring in the area. Detailed qualitative and quantitative phytodiversity spectra per individual island are presented, and floristic dissimilarity (beta-diversity) between islands is considered. Spatial distribution of 28 chorological, ecological, vegetative and reproductive traits for each recorded taxon have been calculated in order to detect regional and fundamental patterns in functional biogeography beyond traditional species-based approaches, based on both taxonomic and functional components of diversity. Mediterranean species constitute the most abundant chorological element and therophytes the most abundant life-form element in the region. Surface area is the most influential variable contributing to species richness; very strong relationships in (1) species per area, (2) functional richness per area and (3) functional richness per species richness are revealed for the Santorini archipelago. Floristic cross-correlations revealed an overall high floristic heterogeneity among the individual islands. The phytodiversity assessment presented is undoubtedly of documentary value in consideration of expected future eruptive events in the area which may damage the plant cover at least on some of the involved islands to a yet unpredictable extent.

Introduction

Islands prevalently function as model systems and natural laboratories for the design of many biogeographical, ecological and evolutionary theories (community assembly theory, island biogeography, metapopulation ecology etc., see Warren & al. 2015). Basic ecological and evolutionary processes have been revealed by studying island ecosystems in particular, since evolution is most forceful on islands, their ecology is often simplified (simplicity of biota) and they are area-defined by distinct natural boundaries (Whittaker & al. 2014).

Related to island quantity, one of the most-membered archipelagos globally is the Aegean archipelago (Greece), comprising more than 7500 islands and islets (Triantis & Mylonas 2009). Since long, the Aegean archipelago has attracted ecologists and biogeographers as it offers an ideal subject for biogeographical, ecological and evolutionary research (see, e.g., Runemark 1969) due to its specific geomorphological and biodiversity features. Multiple topographic heterogeneity, complex geological and palaeogeographic history, highly diverse geological and environmental properties (Sfenthourakis & Triantis 2017), along with the archipelago's geographical posi-

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tion at the junction of the three continents of Europe, Asia and Africa, have resulted in high levels of overall species diversity and rate of endemism (Strid 1996, 2016; Dimopoulos & al. 2013, 2016).

Part of the knowledge derived from over two centuries of botanical and phytogeographical exploration of the Aegean islands (e.g. Rechinger 1944, 1949, 1978; Rechinger & Rechinger-Moser 1951; Runemark & al. 1960; Lack & Mabberley 1999; Kougioumoutzis & al. 2017) has played a key role in the development of modern island biogeography theory (Sfenthourakis & Triantis 2017) and led to the determination of factors influencing the biodiversity, biogeographic patterns, endemism and species-turnover of the flora in the area, either regionally or in comparison with other archipelagos (among others Snogerup & Snogerup 1987, 2004; Höner & Greuter 1988; Raus 1989; Höner 1991; Triantis & al. 2006; Trigas & al. 2007; Triantis & al. 2008; Triantis & Mylonas 2009; Panitsa & al. 2010; Kallimanis & al. 2010, 2011; Kagiampaki & al. 2011; Iliadou & al. 2014; Kougioumoutzis & Tiniakou 2015; Kougioumoutzis & al. 2014, 2017). However, for a significant number of taxa and islands more thorough studies are still needed while some smaller islets have never been floristically explored so far.

Most of the islands of the Aegean archipelago are of continental, but some also of oceanic origin, namely the ones that emerged by intensive volcanic activity (e.g. in the Santorini island complex, Higgins & Higgins 1996). Santorini is the most important of the Quaternary volcanic centres in the Aegean region and belongs geographically to the South Aegean Volcanic Arc (known also as Hellenic Volcanic Arc, Albanakis & Styllas 2004), where subduction of the African Plate under the European Plate is continuously in progress (Fytikas & Vougioukalakis 2005).

Although the surface of any of the eight islands forming the Santorini archipelago is currently made up of volcanic rocks or at least thickly covered by pyroclastic sediments, the volcanic substrate was primarily built on a base of non-volcanic rock, a foundation of marble and schist which is still exposed on the hills around the archaeological site of Ancient Thira, on the main island of Thira. Volcanism started 1.5 million years ago in the S part of this island, but the main phase dates only from 200 000 years ago (Higgins 2009) with the most recent eruption taken place in 1950. The result of this still ongoing volcanic activity in the area (Jenkins & al. 2015; Vougioukalakis & al. 2016) is the formation of two seaborn islands of different size and age, *viz.* Nea Kameni and Palea Kameni. These islands, besides Anak Krakatau (Indonesia), belong to the world's most prominent examples of marine emergent islands serving as unique and typical examples of, and subjects of research on, primary Mediterranean and tropical succession, respectively (Whittaker & al. 1989; Thornton 2007; Dimopoulos & al. 2010). Such islands offer the opportunity to observe the starting point of evolutionary and organismic primary colonizing processes.

Despite its importance for the understanding of fundamental ecological processes, the overall vascular plant diversity account of the Santorini archipelago had not been achieved until recently. Although botanical exploration of the region started already in 1701 (Tournefort 1703) and continued step by step during the 19th, 20th and 21th centuries (the floristic results catalogued ad interim in Friedrich 2004: 244–248), the most complete regional inventory of vascular plants, at the same time considering recent taxonomic and nomenclatural adaptations, is summarized only in this study (see Table S1, supplemental content online) by adding many hitherto unpublished floristic records collected by the present authors (vouchers at B and UPA, herbarium codes according to Thiers 2019+).

In the past two decades there has been an increasing deal of interest in using functional diversity (FD) to get insight into ecosystem functioning because traits not only account for potential functional redundancy (Rosenfeld 2002), but they also provide a mechanistic link to observed diversity effects (Díaz & Cabido 2001). A functional trait approach has now been rapidly developed in plant ecology, facilitated by standardized protocols and methods (Pérez-Harguindeguy & al. 2013, 2016). More recently, a field dedicated to the study of the spatial and temporal distribution of forms and functions of organisms has started to gain biogeographers' attention, termed functional biogeography (Reichstein & al. 2014; Violle & al. 2014; Whittaker & al. 2014), which extends biogeography beyond species-based approaches.

We present the first study analysing plant diversity patterns regarding the Santorini archipelago as a total. Our main objective is to examine elementary biodiversity patterns based on two components of diversity, i.e. taxonomic and functional. Our aims are: (1) to bring together unpublished floristic records generated by the authors during the last eight years, which add substantially to what is known from previous literature for this area; (2) to compile and to make critical use of most recent taxonomic and chorological literature information on the phytodiversity of the investigated area; (3) to analyse the data in order to detect fundamental biodiversity and biogeographical patterns based on both taxonomic and functional components of diversity.

Study area

The Santorini-Christiana island group (36°15'00"N to 36°28'40"N and 25°12'10"E to 25°29'13"E) is a complex of eight islands located in the Aegean Sea, forming the southernmost part of the Kiklades, 260 km SE of Athens and 120 km N of the island of Kriti. The Santorini archipelago is an active volcanic field with many centres of intense volcanic activity resulting from a complex history of volcanic eruptions over the last 1.5 million years with 12 major explosive eruptions within the last 200 000 years, during which the individual islands have changed
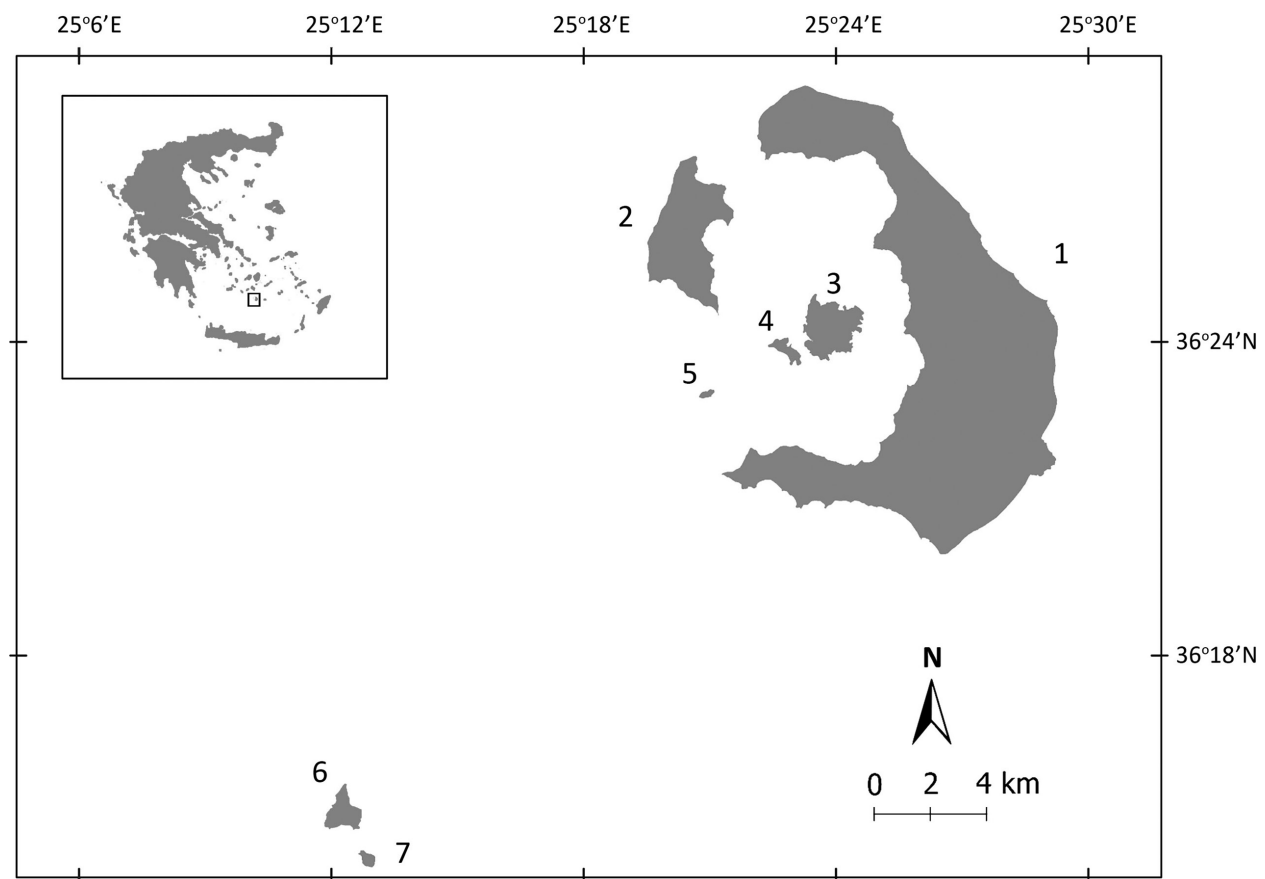
Fig. 1. Map of the Santorini archipelago; the islands carrying vascular plant vegetation are shown. Island numbers, names and abbreviations as follows: 1: Thira (Thi), 2: Thirasia (Thr), 3: Nea Kameni (NK), 4: Palea Kameni (PK), 5: Aspronisi (Asp), 6: Christiani (Chr), 7: Askania (Ask). – Drawing by E. Karadimou. The Hellenic Geodetic Reference System 1987 or HGRS87 was used.

their shape and size repeatedly, resulting in their current configuration (Fig. 1). The crescent-shaped main island, Thira (or commonly Santorini, 76 km^2), is the largest of the complex (N-S extension c. 17 km, W-E extension c. 6 km) and along with Thirasia (9.4 km^2) and Aspronisi (0.13 km^2) situated in a dissected ring around a flooded caldera. The inner caldera cliffs of the ring islands reach a height of up to 400 m above sea level and a depth of c. 390 m below sea level. The caldera is a composite structure that first appeared 25 000 years ago and took its final shape as a result of at least four collapse events (Druitt & Francaviglia 1992). The major intra-caldera eruption, one of the most powerful in the recorded history of the world, occurred around 1645(±4) BC (Hammer & al. 2003), the so-called "Minoan eruption" because it was initially linked to the demise of the Minoan Civilization of the Kiklades and Kriti (among others Bond & Sparks 1976). Nevertheless, a debate is still evolving on the exact time of the great explosion, between a "high" date in the later seventeenth century BC, and a "low" (or conventional) date in the late sixteenth to early fifteenth century (for more details see Pearson 2018; Manning 2014).

The islands of Palea Kameni (0.54 km^2) and Nea Kameni (3.42 km^2) have subsequently emerged in the centre of the caldera between 197 BC and 1950 AD (Fytikas & al. 1990). The two islands represent the peak of an intra-caldera volcanic edifice which is about 4 km wide at its base and has a volume of about 2.5 km³ most of which is under water (rising from the base of the caldera at a depth of about 300 m to a summit of 127 m above sea level on NK).

Three more islands, called the Christiana island group, are located c. 20 km SW of the main island complex, comprising Christiani, the largest one (1.188 km^2), adjacent to it Askania (0.257km^2), and SE of the latter the third, Eschati, which constitutes an isolated cliff bare of vascular plants (Hansen 1971), and hence omitted from Fig. 1. From fossils found in the tuffs it is documented that the Christiana islands are of oceanic origin, too, and hold for the geologically oldest volcanic part of the present Santorini archipelago (Druitt & al. 1999; Friedrich 2000, 2004; Soldatos 2019).

The limestone massif of Mts Profitis Ilias and Mesa Vouno, consisting of upper Triassic to Eocene marbles as remnants of the primary continental, non-volcanic basement of the island, projects from the surrounding volcanic landscape at the widest part of the main island of Thira. This calcareous rock, together with limited layers of slightly metamorphic schist, covers c. 15% of the surface of Thira, another c. 15% are made up by

igneous lava-flows, and c. 70% of the surface of Santorini is occupied by, locally up to 40 m thick, pumice layers (Friedrich 2000). Geographical and ecological parameters of the Santorini archipelago as far as relevant to understand contemporary phytodiversity are summarized in Table 1.

The Santorini Archipelago is subject to the Mediterranean-type winter rain climate. The low amount of rainfall (364 mm/a on Santorini) leads to regular periods of water shortage during summer. However, evaporation from the surrounding sea, as well as regular chill etesian (northeasterly) winds causing fog and frequent dew have a compensational effect on the local hydrology, even facilitating irrigation-free agriculture (Philippson 1959). Perennial surface water courses do not exist in the area.

Thira is extensively cultivated (to c. 80% of the island's surface). Vineyards exist on spacious pumice terraces. Only small areas are used for the cultivation of vegetables and fruits for self-supply – the lack of water is the limiting factor. Agriculturally unfavourable ground is largely sealed with buildings, tourist facilities and traffic zones including an international airport while only few areas are still grazed for traditional animal husbandry (mainly of mules). Thirasia is cultivated to a similar extent, but many fields and terraces are nowadays abandoned. Aspronisi is dominated by steep to nearly perpendicular pyroclastic cliffs, making landings difficult though two narrow pebble beaches and a small provisory anchorage exist on the islet. The island's top (74 m above sea-level) forms a flat plateau made up of a pure, 25 m thick pumice layer which is settled by a sparse vegetation of drought- and salt-tolerant low scrub mixed with short-lived herbaceous therophytes. Aspronisi is currently (and has obviously always been) uninhabited by humans (Philippson 1959).

Nea Kameni (NK) emerged 1570–1573 AD and after seven consecutive eruptive phases took its final shape in 1950 (Druitt & al. 1999). As a result of the last eruption, in 1950, part of the previous lava-flows was covered by fresh pumice ashes of high ecological importance for primary succession processes (Raus 1986, 1988). NK is currently uninhabited, though people from the main island of Thira intermittently maintained cultivations and livestock during past inter-eruptive periods until 1925. Today there exist populations of rabbits and two seagull colonies (*Larus cachinnans*) on the island, but much more manifestly influencing the local ecosystem is the fact that a great many of tourists enter the island year-round by means of guided tours, making NK the most visited island in the area after Thira. Several small anchorages exist on NK, two of them enabling shore leave.

Palea Kameni (PK) was formed by a series of eruptions between 197 BC and 47 AD, with a subsequent explosive eruption of pumice in 726 AD. Volcanic unrest then ceased again until the 1500s, when the neighbouring sea-born sister island Nea Kameni appeared. Some inhabitants from Thira kept livestock during the last century until 1979 on PK, and over the last decade a sole farmer lives permanently on the island maintaining some vegetable plantations and a livestock of goats and pigs that puts severe pressure on PK's actual vegetation of low-growing evergreen maquis with interspersed annual plant communities.

The remote Christiana island group with the islands Christiani and Askania is now uninhabited, but on Christiani there was a human settlement the vestiges of which date back to the Bronze Age (Broodbank 2002). Local agriculture on terraced fields has been abandoned eventually in the 1980s and remained un-farmed since then. Remnants of segetal and ruderal flora are met with even today germinating from the local seed-bank, but pesticides and fertilizers are now absent from this ecosystem.

Material and methods

Phytodiversity survey data

Total floristic inventory of the Santorini archipelago
The current floristic matrix of the individual islands and islets of the Santorini archipelago (Table S1, supplemental content online) includes all hitherto unpublished records and results of the fieldwork conducted by the authors of the present paper between 2010 and 2018, as well as the results of previous floristic explorations from 1897 to 2000 (cumulated by Dumont d'Urville 1822; Heldreich 1899a, 1899b, 1901; Wilski 1902; Vierhapper 1914, 1919; Cammerloher 1935; Hansen 1971; Diapoulis 1971; Rackham 1978; Schmalfuss & al. 1981; Raus 1986, 1988, 1991, 1994; Covillot & al. 1997; Biel 2001, 2005; Katsipis 2004; Dimopoulos & al. 2010; Brullo & Erben 2016). The botanical exploration of the Santorini-Christiana island group, as designed and executed by the present team of authors, is presented in detail in Table S2 (supplemental content online). Previous records from the area of *Hymenonema graecum* (Hansen 1971: 147; Liveri & al. 2018: 8) and *Arthrocaulon macrostachyum* (Hansen 1971: 117, under *Arthrocnemum fruticosum*) are based on misidentified material of *Reichardia picroides* and *Salicornia fruticosa*, respectively (specimens at C!, rev. TR) and are consequently not mapped in Strid (2016: 159, 333) and accordingly deleted from the archipelago's floristic catalogue (Table S1). Literature records from the area of *Limonium graecum* (Rechinger 1944: 429; Hansen 1971: 136; Raus 1991: 119) and *L. roridum* (Strid 2016: 647) are incorrect and refer to *L. thirae* (Brullo & Erben 2016: 143–144, 203). The same is true for previous records of *Limonium ocymifolium* (Covillot & al. 1997: 224; Strid 2016: 646) which refer to *L. archeothirae* (Brullo & Erben 2016: 165–168, 200). Nomenclature, as well as life-form and chorological categories used in Table S1 are taken from Dimopoulos & al. (2013, 2016) and Piirainen & al. (2017), where also nomenclatural authors of plant names are found (omitted from the present paper).

Table 1. Geographical and ecological parameters of the Santorini island group.

	Thira	Thirasia	Aspronisi	Nea Kameni	Palea Kameni	Christiani	Askania
Area [km²]	76.19	9.4	0.13	3.42	0.54	1.188	0.257
Altitude [max., m]	567	294	74	127	98	238	168
Geological evolution	formed c. 3 million y BP (pre-volcanic); first eruptions 2 million – 700 000 y BP (Strongili island); current contour from "Minoan" eruption c. 1645 BC	part of Strongili island; became an individual island c. 30 000 y BP; current contour from "Minoan" eruption c. 1645 BC	part of Strongili island; became an individual island c. 30 000 y BP; current contour from "Minoan" eruption c. 1645 BC	emerged from sea-floor stepwise since 1570 AD; current contour and elevation from eruptions of 1926–1950 AD	emerged from sea-floor 197 BC – 726 AD; current contour from earthquake in 1457 AD	formed c. 700 000 y BP; current contour and elevation from subsequent erosion	formed c. 700 000 y BP; current contour and elevation from subsequent erosion
Surface substrate	pre-volcanic limestone rock and schist, volcanic rocks, igneous lava flows, pyroclastic deposits (mainly from c. 1645 BC)	volcanic rocks, pyroclastic deposits (mainly from c. 1645 BC)	pyroclastic deposits (mainly from c. 1645 BC)	volcanic rocks, igneous lava flows from 1570–1941 AD, pyroclastic deposits from 1950 AD	volcanic rocks, pyroclastic deposits (mainly from 726 AD)	volcanic rocks, pyroclastic deposits (mainly from c. 1645 BC)	volcanic rocks, pyroclastic deposits (mainly from c. 1645 BC)
Distance from main island (Thira) [km]	0	1.72	2.3	1.465	3.92	17.6	18.63
Present population	15 250	319	0	0	1	0	0
Former cultivation	+	+	–	–	+	+	–
Present cultivation	+	+	–	–	+	–	–
Former grazing	+	+	–	–	+	+	–
Present grazing	+ mainly mules & donkeys	+ mainly rabbbits	+ rabbits	+ rabbits	+ goats, pigs	–	–

Table 2. Botanical exploration history of the Christiana island group (southernmost part of the Santorini archipelago).

Date	Researchers	No. of taxa recorded:		Floristic additions per visited island
		Christiani	Askania	
29 Jun 1960	H. Runemark & B. Nordenstam	61	–	61
27 Jun 1967	H. Runemark & B. Bentzer	–	31	31
11 Apr 2017	T. Raus & E. Karadimou	103	–	48
11 Apr 2017	P. Dimopoulos	–	9	5
19 Apr 2018	T. Raus & P. Dimopoulos	69	–	16
20 Apr 2018	E. Karadimou & A. Tourtas	–	78	54

The ring islands: Thira, Thirasia and Aspronisi

After the first collection of a vascular plant species in 1701 (*Sisymbrium orientale*, Tournefort 1703), knowledge on the flora of Thira has been compiled by numerous explorers for almost 300 years now, hence the vascular plant diversity of this island is relatively well known. Exploration of the autochthonous flora of Thirasia started not earlier than in 1819 (Dumont d'Urville 1822; see Rechinger 1944: 852), and the actual number of confirmed species was brought together by hitherto unpublished fieldwork of the senior author (TR) in 1985–1990. The flora of Aspronisi was initially surveyed in 1979 by C. Steidel (Stuttgart), who then collected 17 hitherto unpublished taxa of vascular plants (vouchers at STU, see Schmalfuss & al. 1981: 10). On a second visit, in 1990, one of us (TR) augmented the local vascular plant list by 29 to 46 taxa. Afterwards, Aspronisi became a nesting-ground of a seagull colony (*Larus cachinnans*), not yet present in 1990. In 2017 and 2018 the authors of this paper gained a few shore-bound floristic additions to the list of 1990, but unfortunately were prevented from reaching the island's plateau due to the instability of the nearly vertical slopes. Therefore, they did not manage to record probable additions of ornithochorous taxa to Aspronisi after the establishment of the local seagull colony.

The caldera islands: Palea Kameni and Nea Kameni

The first recorded floristic survey of Nea Kameni (NK) was conducted in April 1911 (Vierhapper 1914, 1919), about 40 years after the vegetation-destructive eruptions of 1866–1870 (Fouqué 1879). Subsequent floristic censuses in the 20th century particularly aimed at documenting possible correlations between phytodiversity and different surface-age of local volcanic substrates (Hansen 1971; Raus 1986, 1988; Sipman & Raus 1995). During the past decade, the island's flora has been systematically monitored by the authors of this paper (for details, see Karadimou & al. 2018). Hansen (1971) contributed the first preliminary notes on the flora of Palea Kameni (PK), much augmented by fieldwork of T. Raus in 1984–1990 and P. Dimopoulos & L. Mucina in 2000 (in summary analysed in Dimopoulos & al. 2010).

The remote islands: Christiani and Askania

The islands Christiani and Askania of the remote Christiana island group (the third islet, Eschati, is bare of vascular plants) were first visited by B. Bentzer, B. Nordenstam and H. Runemark in 1960 and 1967, each time end of June (Hansen 1971). The present authors investigated the islands in April 2017 and 2018, i.e. in a season of the year more suitable for providing floristic evidence under Mediterranean conditions (see Table 2).

Plant functional traits data

Functional traits are morphological, physiological, phenological or behavioural features measured on organisms that can ultimately be linked to their performance (Violle & al. 2007). In trait-based ecology it has been shown that it is possible to aggregate functional traits measured on organisms to explain the functioning of populations to ecosystems and beyond (Violle & al. 2007; Lavorel & Garnier 2002). Trait-based approaches have also been used extensively to describe the diversity of forms and functions within a study unit using different distance metrics (e.g. variance based, see Petchey & al. 2004; Blonder & al. 2014).

Common data types for traits include continuous, categorical, ordinal and binary variable formats. The data type has repercussions for subsequent data analyses. When choosing traits for calculating functional diversity it is important to consider which, and how many, traits are included, as well as what insights they will provide into the ecosystem processes, community structure or assembly processes under consideration (Díaz & Cabido 2001).

Following this approach, we use a set of 28 traits for each recorded infrageneric taxon, assembled by data collected from plant traits databases and literature supplementary to the purpose. We used a wide range of functional characteristics in order to incorporate interactions among species as well as species–environment relations. Traits representing vegetative characteristics – mainly related to the competitive ability of species, growth capability, and disturbance tolerance – include longevity (data from botanical descriptions in relative basic floras by Tutin & al. 1964–1980, 1993; Strid & Tan 1997, 2002; Davis 1965–1988; Pignatti 1982), maximum plant height, mean leaf length, mean leaf width (data from measurements on available plant specimens, as well as from botanical descriptions in relative basic floras mentioned above), leaf length/width ratio (val-

ues calculated), life form (data from Dimopoulos & al. 2013, 2016), growth form (data collected from botanical descriptions in relative basic floras mentioned above), habitat type (data from Dimopoulos & al. 2013, 2016), leaf surface texture, and canopy structure (data collected from measurements on available plant specimens, as well as from botanical descriptions in relative basic floras mentioned above). The ecological preferences of plant taxa include indicator values for soil acidity, soil nutrient content, soil humidity, continentality, soil salt content, light availability, and temperature traits (based on Ellenberg indicator values published in Böhling & al. 2002). Regenerative characteristics – related to species dispersal ability in space and time – include flowering period start, flowering period end, flowering period length (data based on field observations, as well as collected from botanical descriptions in relative basic floras mentioned above), seed production (data collected from botanical descriptions in relative basic floras mentioned above), seed weight (data from the Royal Botanic Gardens Kew Seed Information Database, SID), flower size (data collected from botanical descriptions in relative basic floras mentioned above), flower sex (data from Julve 2019+), flower colour (data based on field observations, as well as collected from botanical descriptions in relative basic floras mentioned above), pollination type (data from Julve 2019+), fruit type, and dispersal mode traits (data botanical descriptions in relative basic floras mentioned above, as well as from Julve 2019+). For more detailed information, see Table S3 (supplemental content online) and Karadimou & al. (2016).

Diversity components quantification

We calculated measures of taxonomic (TD) and functional (FD) alpha (for each individual island) and beta diversity (between each pair of islands). Taxonomic alpha diversity is represented here as species (plus supplemental subspecies) richness, as well as the richness of genera and families. Either dendrograms or functional spaces have been used to estimate functional diversity across space and time (Mouchet & al. 2008; Villéger & al. 2008). Based on this approach, in this study alpha FD is represented by multidimensional indices that explore different facets of functional diversity: (a) functional richness (FRic) (Mason & al. 2005; Villéger & al. 2008), (b) functional dispersion (FDis) (Laliberté & Legendre, 2010), Rao's quadratic entropy (RaoQ) (Rao 1982; De Bello & al. 2010) and (c) the dendrogram-based FD index (FDen) (Petchey & Gaston 2006). FRic and FDen reflect the range of values of the functional traits. RaoQ and FDis reflect both functional richness and divergence, in the sense that they quantify the degree of functional dissimilarity between the members of a community. All calculations were made using the function "dbFD" in the FD package in R (R Core Team 2018). This function computes FD indices using a species-by-traits matrix to compute the Gower dissimilarity when the data comprise different trait types (continuous, ordinal, nominal, or binary) which is the case in our study. The function uses Principal Coordinates Analysis (PCoA) to return PCoA axes, which are then used as "traits" to compute the multidimensional space where each dimension is represented by a trait (or PCoA axis). Moreover, the function allows FRic index values to be standardized by the "global" FRic that include all species, so that FRic is constrained between 0 and 1 and the values comparable to other studies. At the beta diversity level, temporal changes in community composition can be quantified using dissimilarity indices (Hillebrand & al. 2010; Stegen & al. 2013). In order to calculate beta TD and FD, the Jaccard index was used, a binary dissimilarity coefficient that uses presence-absence data (Jaccard 1912). Dissimilarity among two or more assemblages is equal to the ratio between the amount of diversity not shared between assemblages relative to their total diversity. Functional dissimilarity between assemblages can also be estimated by quantifying the dissimilarity in the functional space which each of them occupy. These indices were computed as dissimilarities between islands in R using the "betapart" function of the betapart package. This function allows computing pair-wise dissimilarities (distance matrices) and multiple-site dissimilarities.

Diversity patterns analysis

The relationship between taxonomic and functional diversity
The relationship between taxonomic and functional diversity indices has been used to better describe and understand the structure of biological communities. Functional diversity is expected to have an asymptotic relationship with species richness because at some point, the addition of new species will increase some of the already established functional groups (functional redundancy). A steep slope in the relationship indicates the fast emergence of new functions, whereas a gentle slope implies a greater redundancy of existing functions. Here, we display the relationship between species richness and functional richness, but also functional dispersion and Rao's quadratic entropy in order to compare it with other cases from the literature, since this relationship, although considered fundamental mainly for displaying functional redundancy, is not yet well studied across species, communities, habitats and spatial scales.

The island species–area relationship and the functional diversity–area relationship
The recently introduced concept of the functional diversity–area relationship (FAR, Smith & al. 2013; FDAR, Whittaker & al. 2014), is theoretically based on the same assumptions as the classical species–area relationship (SAR). In this study, we present both island species–area

Table 3. Number of vascular plant taxa (family, genus, species and subspecies level) per individual island in the Santorini archipelago. Species represented by infraspecific taxa in the area are counted by number of subspecies. Taxonomic delimitation according to Dimopoulos & al. (2013).

Island	Families	Genera	Infrageneric taxa (species incl. supplemental subspp.)	%
Archipelago	88	348	696	100
Thira (Thi)	85	329	653	93.8
Thirasia (Thr)	50	193	278	39.9
Nea Kameni (NK)	39	126	195	28.0
Palea Kameni (PK)	42	128	186	26.7
Christiani (Chr)	42	119	159	22.8
Askania (Ask)	34	74	91	13.1
Aspronisi (Asp)	21	44	56	8.1

Beta taxonomic diversity (TD) – functional dissimilarity (FD) among islands
Beta TD among the individual islands of the archipelago was calculated as Jaccard's dissimilarity index (Jaccard 1912), using beta.pair function of the betapart package (Baselga & Orme 2012) in R (R Core Team 2018). Moreover, the same index was used to calculate FD according to the framework introduced by Villéger & al. (2011), using the functional.beta.pair function of the betapart package (Baselga & Orme 2012) in R.

relationship (ISAR) and island functional diversity–area relationship (IFDAR) and compare the resulting curves to detect whether there are any similarities in these patterns between the two components of diversity by using the logarithmic form of the power function $\log S = \log c + z \log A$ (Arrhenius 1920, 1921: $\log_{10}$-transformed values of species and area). Since the space of the linearized power function is not arithmetic but logarithmic, z can be interpreted as a scaling factor describing how fast the response of species richness to area changes along the SAR curve is (Lomolino 2001).

Results

Overall diversity of the Santorini archipelago

The vascular plant diversity of the seven vegetated islands of the Santorini Archipelago consists of 80 families, 336 genera, 682 infrageneric taxa (species plus supplemental subspecies) of angiosperms, 3 families, 4 genera, 4 species of gymnosperms and 5 families, 8 genera, 11 species
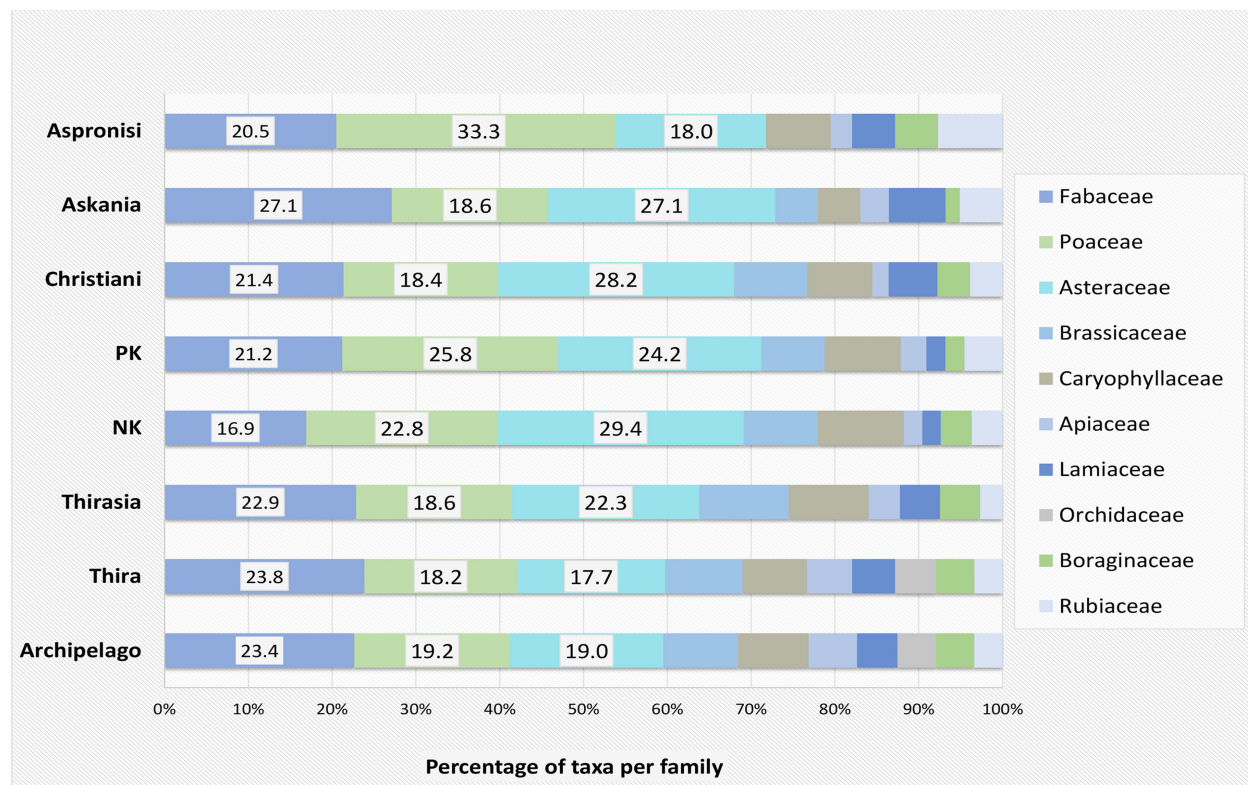

Fig. 2. Overall portions of the 10 most species-rich vascular plant families recorded from the individual islands of the Santorini Archipelago. Percentages (%) are specified for the quantitatively top three (*Fabaceae*, *Poaceae*, *Asteraceae*).
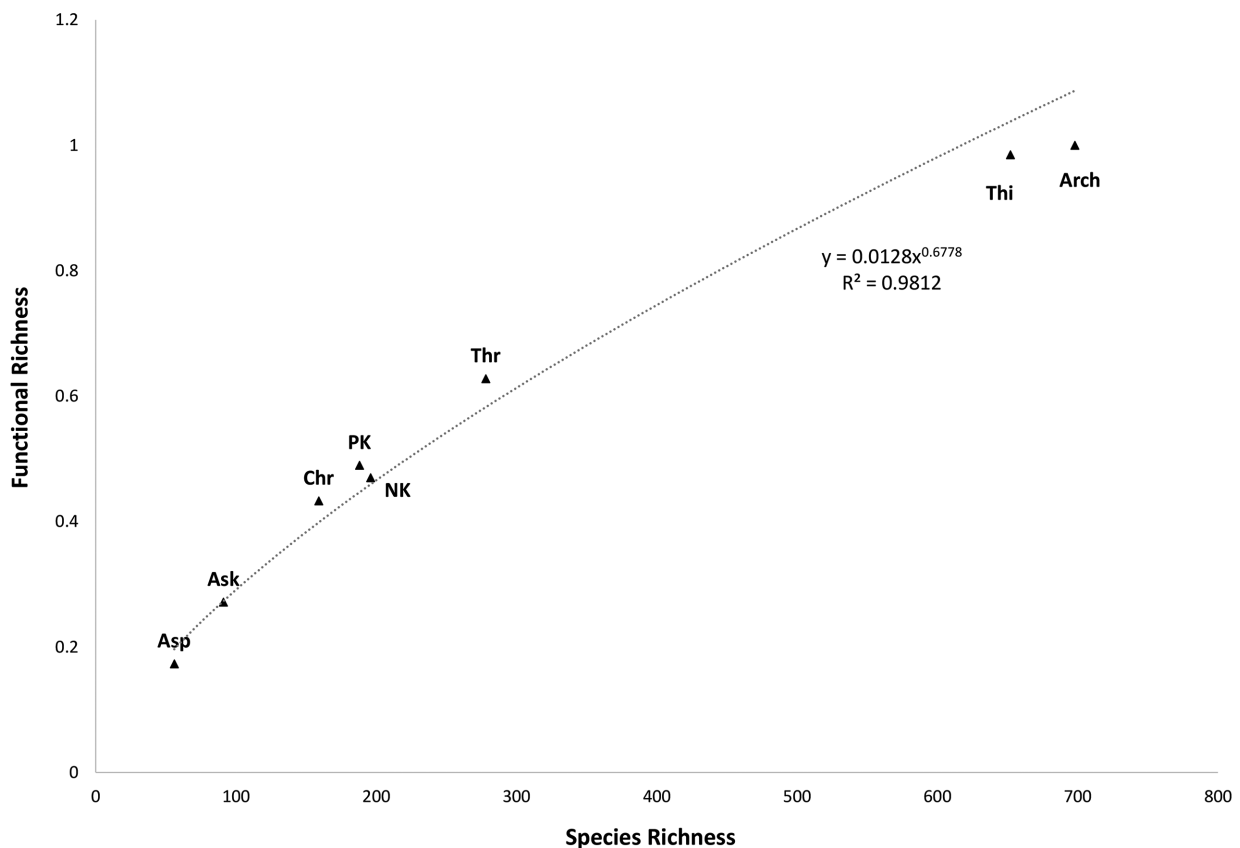
Fig. 3. The relationship between species richness and functional richness for the seven islands of the Santorini Archipelago. Island numbers, names and abbreviations as follows: Thira (Thi), Thirasia (Thr), Nea Kameni (NK), Palea Kameni (PK), Aspronisi (Asp), Christiani (Chr), Askania (Ask), total archipelago (Arch).

of pteridophytes (taxa delimitation after Dimopoulos & al. 2013). The floristic diversity as distributed in the three sub-groups of the Santorini archipelago (ring islands, caldera islands, Christiana islands) is given below:

- Ring islands: a cumulative total of 661 taxa of ferns and flowering plants have been found, i.e. 653, 278 and 56 taxa in Thira, Thirasia and Aspronisi, respectively.
- Caldera islands: cumulatively 255 taxa have been found, i.e. 195 taxa in Nea Kameni and 186 taxa in Palea Kameni. Both islands share 126 taxa.
- Christiana islands: cumulatively 171 taxa have been found, i.e. 159 taxa in Christiani and 89 taxa in Askania. Both islands share 77 taxa.

A detailed quantitative distribution of families, genera and infrageneric taxa (species with supplemental subspecies added) per individual island and in the Archipelago as a total, and the infrageneric taxa in each island as a proportion of the total number of taxa in the Archipelago are presented in Table 3; the proportion is an indication of the contribution of each island to the floristic diversity of the whole Santorini archipelago.

From the analysis of the taxon richness per family per individual island in Fig. 2, it is evident that the three most species-rich families in the area are *Fabaceae* (97 infrageneric taxa, 23%), *Poaceae* (80 infrageneric taxa, 18%) and *Asteraceae* (78 taxa, 18%) which altogether cover c. 60% of the vascular plant diversity of each of the individual islands (Fig. 2). The distribution of genera is presented in Fig. S1 (supplemental content online).

Relationship between taxonomic and functional diversity

The relationship between species richness and functional richness for the seven vegetated islands of the Santorini archipelago is presented in Fig. 3. The type of curve describes an ecosystem where functional diversity increases more rapidly at low species diversity and subsequently increases at declining rates as and when the number of functions represented in the assemblage becomes important. The two diversity indices showed a significant positive relationship that did not reach an asymptote, suggesting low functional redundancy in the plant assemblages of the seven islands. Nevertheless, Functional Dispersion and Rao's Quadratic entropy indices did not display a significant positive relationship with species richness. In fact, dispersion values do not change with increased species richness (not shown).

Chorological and life-form spectrum − endemism

Mediterranean species constitute the most abundant chorological element in the Santorini archipelago as expected (Table 4), and therophytes the most abundant life-form element (Table 5). A similar pattern is presented in the spectra of the individual islands of the archipelago (Fig. S1 & S3, supplemental content online). Nevertheless, three of the seven islands (Christiani, Askania and Aspronisi) display a percentage of Mediterranean species higher than 50% compared to the rest, while another subgroup of islands (NK, PK and Aspronisi) displays the highest percentage of therophytes (>70%).

The Greek element of the area is represented by 30 taxa (4.3%), five (5) of which (including *Pimpinella pretenderis* which is only doubtfully given for the Cretan area) are found exclusively in the phytogeographical region of the Kiklades (Table 6). According to Dimopoulos & al. (2018), 1791 taxa are found in the phytogeographical region of the Kiklades, 168 of which are considered Greek endemics (9.4%). The existence of biregional endemics is a good indication of phytogeographical connections between regions (Georghiou & Delipetrou, 2010). Based on the geographical distribution of nine (9) of the endemic species corresponding to one or two phytogeographical areas presented in Table 6 (*Aegilops biuncialis* subsp. *archipelagica*, *Eryngium amorginum*, *Erysimum senoneri* subsp. *senoneri*, *Filago aegaea* subsp. *aegaea*, *Filago cretensis* subsp. *cycladum*, *Ornithogalum creticum*, *Pimpinella pretenderis*, *Silene cythnia* and *Trifolium praetermissum*), we could claim that the Santorini archipelago is chorologically equally closely connected to the East Aegean Islands (EAe) and the Cretan area (KK).

The effect of island area

Taxonomic and functional diversity

The logarithmic species–area relationship (SAR), as well as the relationship between the other taxonomic groups (families, genera and infrageneric taxa: species and supplemental subspecies) and area for the Santorini archipelago are presented in Fig. S4 (supplemental content online). The SAR model explains 95.7% of the variability of species richness, as well as 0.93 and 0.89 of the genera and families of the Archipelago. The z-parameter of the linearized power function of the ISAR model for the Santorini archipelago is z = 0.34. The corresponding values for the genera and families of the Archipelago are lower: 0.27 and 0.18, respectively. The logarithmic island

Table 4. Chorological spectrum of the vascular flora of the Santorini archipelago, for the most abundant chorological categories.

Chorological category	Number of infrageneric taxa	Percentage (%) for the total archipelago
Mediterranean	265	38.1
East Mediterranean	68	9.8
European-Southwest Asian	68	9.8
Mediterranean-Southwest Asian	67	9.6
Mediterranean-European	55	7.9
Greek endemic	30	4.3
Cosmopolitan	27	3.9
Palaeotemperate	25	3.6
Mediterranean-Atlantic	22	3.2
Balkan-Anatolian	9	1.3
Subtropical-tropical	9	1.3
Other	51	7.2

Table 5. Life-form spectrum of the vascular flora of the Santorini archipelago.

Life-form category	Number of infrageneric taxa	Percentage (%) for the total archipelago
Therophyte	409	58.2
Hemicryptophyte	107	15.2
Geophyte	85	12.1
Chamaephyte	57	8.1
Phanerophyte	42	6.0
Aquatic	3	0.4

functional richness–area relationship (IFDAR) model explains 88.9% of the variability of functional richness (Fig. S5, supplemental content online). The z-parameter of the linearized power function of the IFDAR model the for the Santorini archipelago is z = 0.22.

Floristic similarity among the islands of the Santorini archipelago

Taxonomic diversity

The number of shared infrageneric taxa (species incl. supplemental subspecies, see Table 3) among islands is summarized as follows: 326 taxa (46.7%) have been recorded on a single island, 125 taxa (17.9%) on two islands, 99 taxa (14.1%) on three islands, 60 taxa (8.5%) on four islands, 37 taxa (5.3%) on five islands, 35 taxa (5%) on six islands and 16 taxa (2.2%, i.e. *Asparagus horridus*, *Atriplex halimus*, *Brachypodium distachyon*, *Crepis multiflora*, *Geranium molle*, *Lagurus ovatus*, *Parietaria cretica*, *Plantago weldenii*, *Polycarpon tetraphyllum*, *Psilurus incurvus*, *Rostraria cristata*, *Senecio leucanthemifolius*, *Silene colorata*, *Stipa capensis*, *Valantia hispida* and *Trifolium scabrum*) on all seven islands.

Table 6. Distribution of Greek endemic taxa in the study area (Dimopoulos & al. 2013). Thi = Thira; Thr = Thirasia; Asp = Aspronisi; NK = Nea Kameni; PK = Palea Kameni; Chr = Christiani; Ask = Askania; IoI = Ionian Islands; NPi = Northern Pindos; SPi = Southern Pindos; Pe = Peloponnisos; StE = Sterea Ellas; EC = East Central Greece; NC = North Central Greece; NE = North East Greece; NAe = North Aegean islands; WAe = West Aegean Islands; Kik = Kiklades; KK = Kriti and Karpathos; EAe = East Aegean Islands; ? = doubtfully present.

Taxon	Islands of the Santorini archipelago							Distribution in Greece (= total area)
	Thi	Thr	Asp	NK	PK	Chr	Ask	
Aegilops biuncialis subsp. *archipelagica*	+	+				+		Kik, KK
Anthemis werneri subsp. *werneri*	+				+			NAe, EC, WAe, Pe, Kik
Atriplex recurva	+							NAe, WAe, StE, Kik, KK
Carthamus leucocaulos	+	+						WAe, EAe, Pe, Kik, KK
Centaurea raphanina subsp. *mixta*	+	+	+				+	StE, WAe, EAe, Pe, Kik
Chondrilla ramosissima	+							EC, WAe, StE, Pe, KK
Crepis neglecta subsp. *graeca*	+					+	+	NC, EC, NAe, SPi, StE, WAe, Pe, Kik
Crocus cartwrightianus	+							StE, WAe, Pe, Kik, EAe, KK
Crocus laevigatus	+							NAe, StE, WAe, Pe, Kik, EAe, KK
Crocus tournefortii	+							Pe, Kik, EAe, KK
Eryngium amorginum							+	Kik, KK
Erysimum senoneri subsp. *senoneri*	+	+		+				WAe, Kik
Filago aegaea subsp. *aegaea*	+		+			+		EAe, Kik, KK
Filago cretensis subsp. *cretensis*	+			+	+			NAe, WAe, EAe, Pe, Kik, KK
Filago cretensis subsp. *cycladum*				+	+	+		EAe, Kik, KK
Limonium aegaeum	+	+						StE, WAe, Pe, EAe, Kik, KK
Limonium archeothirae	+		+					Kik
Limonium proliferum	+							StE, WAe, EAe, Kik, KK
Limonium thirae	+	+			+	+	+	Kik
Muscari cycladicum subsp. *cycladicum*	+							Kik
Nigella degenii subsp. *degenii*	+	+			+			Kik
Nigella doerfleri	+							NAe, Pe, Kik, KK
Ornithogalum creticum	+							Kik, KK
Phleum exaratum subsp. *aegaeum*	+	+	+			+		IoI, NAe, EAe, Pe, Kik, KK
Pimpinella pretenderis	+							Kik, ?KK
Scorzonera araneosa	+	+						Kik, KK
Scorzonera cretica	+							EAe, Pe, Kik, KK, ?NPi
Silene cythnia	+							Kik, EAe
Silene sartorii	+	+						StE, Pe, Kik, KK
Trifolium praetermissum	+							Kik, EAe, KK

The exact number of shared infrageneric taxa between the individual pairs of islands are presented in Table 7. Single island occurrences of monitored taxa are either bound to habitats not extant elsewhere in the Santorini archipelago (e.g. a brackish waterbody and shaded rock gorges on PK) or result from isolated local seedbanks reflecting different crop history of abandoned agricultural sites on individual islands. Another portion of current single island occurrence may reflect recent far-distance immigration with spread to more than one island of the archipelago to be expected. We mention taxa hitherto not found on the main island of Thira, viz. on Thirasia *Aptenia cordifolia* and *Limonium narbonense*, on Aspronisi *Avena barbata* subsp. *wiestii*, on Nea Kameni *Centranthus calcitrapae*, *Crassula tillaea*, *Erigeron canadensis*, *Erodium moschatum*, *Filago minima*, *Paronychia echinulata*, *Poa annua*, *Solanum villosum* and *Suaeda maritima*, on Palaea Kameni *Asplenium obovatum*, *Catapodium balearicum*, *Cymodocea nodosa*, *Datura innoxia*, *Fumaria bastardii*, *Ruppia cirrhosa* and *Torilis webbii*,

Table 7. Floristic similarities between all possible pairs of the studied islands regarding the number of infrageneric taxa in common.

	Thirasia	Aspronisi	Nea Kameni	Palea Kameni	Christiani	Askania
Thira	272	54	176	169	145	82
Thirasia		49	136	132	110	64
Aspronisi			35	39	39	29
Nea Kameni				126	80	48
Palea Kameni					90	61
Christiani						77

Table 8. Floristic dissimilarities (beta-diversity) between the studied islets according to the 1 − Jaccard dissimilarity coefficient.

	Thirasia	Aspronisi	Nea Kameni	Palea Kameni	Christiani	Askania
Thira	0.42	0.58	0.60	0.64	0.78	0.85
Thirasia		0.43	0.43	0.50	0.65	0.71
Aspronisi			0.34	0.55	0.67	0.72
Nea Kameni				0.48	0.56	0.68
Palea Kameni					0.38	0.64
Christiani						0.61

Table 9. Functional dissimilarities (functional beta-diversity) between the studied islands according to the 1 − Jaccard dissimilarity coefficient.

	Thirasia	Aspronisi	Nea Kameni	Palea Kameni	Christiani	Askania
Thira	0.57	0.68	0.69	0.74	0.85	0.91
Thirasia		0.24	0.27	0.36	0.61	0.78
Aspronisi			0.03	0.13	0.44	0.65
Nea Kameni				0.11	0.44	0.64
Palea Kameni					0.39	0.59
Christiani						0.30

dissimilarity coefficient indicate values from 0.11 to 0.91, thus the functional diversity of the studied islands differ from each other from 11% to 91% (Table 9). Higher percentage of functional dissimilarity is recorded between the main island and the two most distant islands (Christiani, Askania). The flora of Askania displays the highest overall functional dissimilarity compared to any of the other six islands' floras (percentage higher that 60% in all cases) apart from its direct neighbour, Christiani. Notably, NK, PK and Aspronisi are the three most functionally similar islands in terms of plant diversity.

Discussion

Overall diversity of the Santorini Archipelago

The Santorini archipelago is a rare case of a seaborn volcanic island group worldwide. In the perspective of testing fundamental biogeographical hypotheses, knowledge of past, current and future status of biodiversity is crucial. Plant diversity has been studied partially on the archipelago (mainly on its largest island, Thira) by numerous explorers for almost 200 years now, particularly providing the opportunity of monitoring primary succession and vegetation recovery after the numerous volcanic disturbances on the geologically young Nea Kameni island (see Karadimou & al. 2018). Arrival history, although fundamental in the process of building up a network of ecological interactions, is poorly known except for NK. Both this process and the resulting species composition may be greatly influenced by the order and timing of arrivals, and by the ecological characteristics of both newly arriving and established taxa (e.g. Fukami 2010).

This is the first time that the vascular plant diversity of the seven vegetated islands of the Santorini archipelago (Aegean Sea, Greece) has been examined as a whole, and the first attempt to analyse vascular plant diversity patterns in this area.

on Christiani *Adonis microcarpa*, *Anchusa stylosa* subsp. *spruneri* and *Cotula coronopifolia*, and on Askania *Eryngium amorginum* and *Fagonia cretica*.

Floristic correlations (taxonomic beta-diversity) between the studied islands by means of the 1 - Jaccard dissimilarity coefficient indicate values from 0.38 to 0.85, thus the floras of the studied islands differ from each other from 38% to 85% (Table 8). Higher percentage of dissimilarity is recorded between the main island and the two most distant islands (Christiani, Askania). The flora of Askania displays the highest overall dissimilarity compared to any of the other six islands' floras (percentage higher that 60% in all cases). Notably, the flora of Christiani is similar to the flora of PK by a percentage of 62%.

Functional diversity
Functional correlations (functional beta-diversity) between the studied islands by means of the 1 - Jaccard

On the Santorini archipelago, *Fabaceae* is the dominant family, followed by *Poaceae* and *Asteraceae*, in contrast to other Aegean regions (or individual islands), or the Greek territory in general, where *Asteraceae* dominate. This is attributed to the fact that the Santorini archipelago consists nearly entirely of volcanic substrates poor in nitrogen which favours the predominance of legumes over other families since legumes have the inherent advantage of taking more nitrogen from the subsoil due to their symbiotic bacteria. These three most common families in the area are known to be best adapted to the ecological conditions of the Mediterranean area, as many floristic studies in Greek insular areas corroborate (among others Panitsa & Tzanoudakis 2001; Kougioumoutzis & al. 2012; Iliadou & al. 2014).

The high percentage of Mediterranean therophytes reflects the Mediterranean character of the vascular flora of the Santorini archipelago. In this context, high proportions of therophytes and legumes indicate the extreme environmental conditions and an overall disturbance in Mediterranean ecosystems (Naveh 1974; Barbero & al. 1990; Panitsa & al. 2003), since therophytes are very typical of desert environments and cultivated land. The decrease of former vigorous farming and cultivating activities on Thira and Thirasia could have led to a partially alteration of the vascular flora of these two largest islands of the archipelago, evidenced by a now relatively high participation rate of the European-Southwest Asian chorological element (9.5 %). Nevertheless, on the smaller islands of the Archipelago, NK, PK and Aspronisi, with relatively little disturbance through settlements and cultivation and with the highest proportion of therophytes, the effect of the extreme environmental conditions on the flora is strongly depicteThe level of Greek endemism in the Santorini archipelago is not high compared to the whole of Greece (22.2 %, Dimopoulos & al. 2013) or to selected other Aegean islands (e.g. Kithira and its off-shore islets, Panitsa & al. 2004; Folegandros, Kougioumoutzis & al. 2015) but is not much lower than in other islands which form the South Aegean Volcanic Arc, such as Anafi (5.6 %, Kougioumoutzis & al. 2012) and Kimolos (6.9 %, Kougioumoutzis & al. 2015). Nevertheless, the level of Greek endemism in the Santorini archipelago is equal or even higher compared to that of the Kiklades phytogeographical region (Kougioumoutzis & al. 2015) with overall similar characteristics, such as small surface area, unfavourable arid climate, and/or intense human pressure (i.e. high intensity of grazing and high amount of cultivated and sealed areas).

The Santorini archipelago tends to be chorologically more closely connected to the East Aegean Islands (EAe) and the Cretan area (KK), based on the evaluation of biregional endemics of the areas compared. In general, according to Georghiou & Delipetrou (2010), the phytogeographical area of the Kiklades islands (Kik) is chorologically more closely connected to EAe than to KK.

Kougioumoutzis & al. (2015) found that Folegandros (a part of Kik like the Santorini island group) is phytogeographically closer to KK than to EAe.

The effect of island area

Surface area is the most influential variable contributing to species richness (Whittaker & Fernández-Palacios 2007). Accordingly, area constitutes a very important parameter regarding the patterns of insular plant diversity in the Aegean (e.g. Panitsa & al. 2006; Kallimanis & al. 2010). A very strong species–area relationship is revealed for the Santorini archipelago with the ISAR model indicating an $R^2 = 0.95$. Kreft & al. (2008) gave an $R^2 = 0.66$ for 488 islands distributed around the globe. Our results are consistent with the value calculated for the East Aegean Islands ($R^2 = 0.893$, Panitsa & al. 2010), for the South Aegean Islands ($R^2 = 0.85$, Kagiampaki & al. 2011) and for some of the West Aegean Islands ($R^2 = 0.947$, Trigas & al. 2008).

The logarithmic approach of the power function ($S = cAz$) of Arrhenius's model (Arrhenius 1921) indicates higher slopes for island-like species–area relationships compared to mainland relationships (Rosenzweig 1995). This logarithmic model has been shown to explain best the variation in species richness (Willerslev & al. 2002). The slope (z-value) shows the increasing rate of species richness with area, and its value depends on the examined geographical unit and the taxonomic group analysed (MacArthur & Wilson 1967). The z-parameter of the ISAR model for the Santorini archipelago (z = 0.34) is higher than the "canonical" value of 0.263 introduced by Preston (1962) and MacArthur & Wilson (1967) but is consistent with the values observed in extremely heterogeneous and isolated floras as it falls within the limits (z =0.2–0.5) given by Rosenzweig (1995) for isolated island groups. Moreover, the z-parameter is close to that reported for the South Aegean Volcanic Arc (z = 0.39 , Kagiampaki & al. 2011) and the East Aegean Islands (0.326, Panitsa & al. 2010) as well as for some West Aegean Islands (z = 0.281, Trigas & al. 2008), while it is lower than that given for 86 islets of the East Aegean (z = 0.40, Panitsa & al. 2006). Notably, the phytogeographical region of the Central Aegean (Kik) as a whole displays a higher z-value (z = 0.434, Kougioumoutzis 2014).

Consequently, while the phytogeographical region of the Kiklades is characterized as having a more isolated flora than the phytogeographical region of the East Aegean Islands and the islands of the South Aegean (Kougioumoutzis 2014), the Santorini island group does not display this distinctive feature, rather various volcanic islands around the globe exhibit comparable z-values (Kreft & al. 2008).

Analysis of species-diversity patterns of remote islands has been crucial to the development of biogeographic theory, but there is limited knowledge on corresponding functional traits patterns on islands. The

parameters of the model describing the relationship between functional richness and area have not been studied sufficiently (e.g. Whittaker & al. 2014).

Here, a strong island functional richness–area relationship (IFDAR) is revealed for the Santorini archipelago with the ISAR model indicating an $R^2 = 0.88$ (lower than the corresponding ISAR) and a $z = 0.22$. This means that as area increases, the number of species increases by a higher rate compared to the functional richness of these species. Additionally, the strong relationship between functional richness and species richness is described by a power model with $R^2 = 0.96$. An important element in this relationship is the presence of an asymptote, since it indicates functional redundancy. The Santorini IFDAR does not display an asymptote; thus, it does not reveal functional redundancy, leading to the hypothesis that a part of the available functional space is not yet occupied by species, but also to a general probability of plant functional traits loss with taxa loss within the community. Other facets of functional diversity besides functional richness, and in particular functional dispersion (which depicts the degree of functional trait dissimilarity between the members of a community, depicted by FDis and RaoQ entropy indices) do not change with increasing island area, which means that trait similarity does not change within the archipelago (compared to floristic and functional richness which increase with increasing area).

Floristic similarity among the islands of the Santorini archipelago

Floristic cross-correlations of the studied islands (beta diversity) using the Jaccard similarity coefficient, revealed an overall high floristic heterogeneity among the individual islands of the archipelago, higher than it has been revealed for instance in East Aegean islet groups (Panitsa & Tzanoudakis 2001). Furthermore, based on the number of islets on which each taxon occurs, nearly half of the taxa occur in only one of the islets and only a small percentage of taxa (2.29%) occurs in any island of the archipelago. The distance between pairs of islands did not affect their floristic similarity. Moreover, floristic heterogeneity was consistent with a functional heterogeneity in most cases.

According to Panitsa & Tzanoudakis (2010), the ratio of the number of species per surface unit is an important parameter of the Aegean vascular plant diversity. The Santorini Archipelago displays a high number of taxa per surface unit (7.6 species/km²) compared to other individual islands of the Kiklades, such as Andros or Naxos (2.7 and 2.4 species/km², respectively, Kougioumoutzis & al. 2015). Nevertheless, this number is lower than the recorded ratio in other islands such as Folegandros, which is considered a biodiversity hotspot (8.55 species/km², Kougioumoutzis & al. 2015). This could be the result of the intense human presence on the largest island of the Archipelago, Thira, since the ratio is much higher than in the rest of the islands.

Epilogue

Already thirteen years ago Pyle & Elliott (2006) calculated for an instant eruption of the Santorini volcano an eruptive phase of more than two years and an uplift of a new lava dome of c. 125 m, stating that the next eruption will be anticipated some days to weeks in advance by discoloration of the sea and a general uplift of the volcanic edifice. In 2011 and the first half of 2012 Santorini experienced its first severe seismo-volcanic unrest since 1950, as detected by permanently installed stations of a monitoring network (Vougioukalakis & al. 2016). Ash and gas hazard is likely to be of concern in a coming eruption from the Santorini caldera. For this, a "most likely" eruption scenario was developed by Jenkins & al. (2015), characterized by slow lava extrusion over periods of one to two years with weak but persistent explosions and ash venting up to 3 km. Higher hazard may be expected to the south and east of the caldera, notably at important tourist and transport areas of Thira, namely the main harbour of Athinios, not to speak of the intra-caldera islands of Nea and Palea Kameni. The actual assessment of the vascular plant diversity and functional biogeography of the Santorini island group, as given in the present study, is therefore undoubtedly of documentary value in consideration of expected future eruptive events in the area which may damage the plant cover at least on some of the involved islands to a yet unpredictable extent.

Acknowledgements

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