Functional diversity changes over 100 yr of primary succession on a volcanic island: insights into assembly processes

E. Karadimou [iD],[1],† A. S. Kallimanis [iD],[2] I. Tsiripidis,[2] T. Raus,[3] E. Bergmeier,[4] and P. Dimopoulos[1]

[1]*Department of Biology, University of Patras, GR-26504 Rio, Patras, Greece*
[2]*School of Biology, Aristotle University of Thessaloniki, GR-54124 Thessaloniki, Greece*
[3]*Botanischer Garten und Botanisches Museum Berlin-Dahlem, Freie Universität Berlin, Königin-Luise-Straße 6-8, 14191 Berlin, Germany*
[4]*Department of Vegetation and Phytodiversity Analysis, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany*

Abstract. Changes in species diversity following volcanic eruptions have been studied extensively, but our knowledge on functional diversity and community assembly under such conditions is very limited. Here, we study the processes following the destruction of vegetation after a volcanic eruption. Specifically, we investigate (1) the temporal patterns of taxonomic and functional diversity over time since a previous eruption (alpha diversity) and beta diversity, (2) the temporal patterns of 26 individual traits (vegetative characteristics, plant taxa ecological preferences, and regenerative characteristics) providing more detailed information on species strategies at the initial and later stages of succession, and (3) the processes driving species assembly and whether they changed over time since the eruption an eruption. We analyzed data recorded during five floristic censuses that took place between 1911 and 2011, calculated alpha and beta facets of taxonomic and functional diversity and examined how community structure changed over time, using 26 functional characteristics, based on their ability to discern primary from later colonists, including longevity, growth form, Ellenberg's indicator values, seed production and weight, flower size and sex, pollination type, and dispersal mode. Null model analysis was used to test whether the observed functional diversity deviates from random expectations. Alpha diversity, both taxonomic and functional, increased over time after an eruption, while beta diversity did not display a clear trend. This finding indicates that mainly abiotic processes determine species assembly over time after an eruption (at least for the time span studied here), contrary to theoretical expectations. It is most interesting that, simultaneously, some aspects of diversity indicated the effect of biotic interactions (facilitation and competition) on the assembly of species a few years after an eruption. This finding implies a legacy effect, since a high percentage of perennial species was noticed in the assemblage right after the eruption, as well as the effect of the harsh environmental conditions on the assembly of the plant communities. In conclusion, our results indicate the role of legacy effects in succession (most probably through the survival of underground plant parts) and underline the importance of disturbance history in providing the context needed for understanding effects of past events on succession.

Key words: beta diversity; community assembly; functional dispersion; functional richness; Mediterranean volcanic island; post-volcanic plant establishment; Santorini archipelago; vegetation succession.

† **E-mail:** ekaradimou@upatras.gr

INTRODUCTION

Ecological succession is a central theme in ecological research for over a century (Walker and Del Moral 2003). Scientists still debate about how species assemble in communities and how ecosystems change following a disturbance. Recently, trait-based approaches have been used to investigate these assembly processes (Mouchet et al. 2010). Community assembly and succession studies incorporate factors such as dispersal, environment, biotic interactions, and stochastic events (Diamond 1975, Whittaker 1992, Thornton 2007). Studies on ecological succession on new volcanic substrata (e.g., Anak Krakatau) argue that species dispersal ability defines colonization patterns of pioneer species on new substrates (Whittaker et al. 1995, Thornton 2007). Primary colonists have traits that maximize dispersal and allow growth on dry infertile substrata (Thornton 2007). Shrubs are common primary colonists in rocky situations, biennial or perennial herbs on gravels, and grasses on silty substrata (Diamond 1975, Whittaker 1992, Thornton 2007). Under this point of view, abiotic factors (i.e., environmental filters) may drive early stages of succession, resulting in species assemblages with traits (like dispersal mode, growth on infertile substrates, etc.) that are more similar than expected by chance (Cornwell et al. 2006). As succession proceeds, biotic interactions (e.g., competition, facilitation) become increasingly important (Callaway and Walker 1997). Interspecific competition (a common type of biotic interaction) may lead to the exclusion of species that are functionally similar, resulting in species co-occurring that are less similar than expected by chance, a result that is commonly described as limiting similarity (Macarthur and Levins 1967, Weiher and Keddy 1995). Species following primary colonists generally have high growth rates, while woody vegetation develops only when there are adequate nutrients (Tsuyuzaki and Moral 1995, Thornton 2007). Stochastic (neutral) processes, independent of species traits, might also drive community assembly (Hubbell 2001). In this case, the diversity of functional traits would be intermediate between habitat filtering and competition (Mouchet et al. 2010). Permanent plots studies, although more rare because vegetation changes slowly, are a more reliable alternative to chronosequence studies since they eliminate assumptions based on space-for-time substitutions (Bakker et al. 1996) and can be used to explore assembly rules (del Moral 2009). Such studies on volcanic substrates have shown that in the early stages of primary succession, when biotic interactions are weak, several other factors such as landscape or priority effects can alter establishment and hinder convergence (Magnússon et al. 2014, Buma et al. 2017, del Moral 2009). Recently, Meiners et al. (2015a) have developed a process model template of succession based on three basic filters combining previous findings: the site conditions and history, the species availability, and the species performance.

A few empirical studies argue that in early succession during the stand-initiation phase, stochastic processes (including colonization stochasticity) predominate (Kunstler et al. 2012). Others argue that all these factors occur simultaneously, or even switch, along environmental gradients (Helmus et al. 2007). Such processes have been poorly explored through the lens of the modern trait-based approach. A few recent studies have quantified temporal changes in plant functional diversity during succession, giving contradictory results (Swenson et al. 2011).

Recently, studies on community assembly along succession use time series of vegetation data combining different facets of diversity, that is, alpha and beta components of taxonomic, functional, and phylogenetic diversity (Purschke et al. 2013, Letten et al. 2014, Karadimou et al. 2016). Purschke et al. (2013), studying secondary succession, found that deterministic processes generate biodiversity during post-disturbance ecosystem development and that abiotic filtering plays an important role in community assembly during the early and early-mid stages of arable-to-grassland succession, whereas the relative importance of competitive exclusion increases in the later successional stages. Similarly, communities generally became more phylogenetically over-dispersed over the course of primary succession in a newly formed habitat, although this pattern did not hold across the disturbance gradient (Chang and HilleRisLambers 2016).

The island of Nea Kameni (NK) of the Santorini archipelago (Cyclades, Greece) constitutes a case study for both Mediterranean vegetation succession patterns and the reassembly of biota

after volcanic eruptions, in correspondence with Krakatau Islands for tropical succession (Whittaker et al. 1989, Thornton 2007). The existence of a long-temporal floristic data series, since 1911, for NK provides the rare opportunity to study for the first time the community assembly and the successional processes occurring on a Mediterranean sea-born volcanic island. The vegetation of NK is currently in a state of recovery after a series of eruptions (from 1570 to 1950) that shaped the island's current form. NK's continuing volcanic activity (analogous to Anak Krakatau) complicates comparisons of plant assembly by imposing periodic disturbance (of varying extent and severity) to the successional processes occurring on the island. By incorporating empirical data representing a long period (they extent over 100 yr and reach up to 83 yr after an eruption), this study offers a comprehensive assessment of primary succession dynamics in both taxonomic and functional community structure on volcanic substrata.

The selection of traits in this study was based on their ability to discriminate between early- and late-successional species according to their functional characteristics. Contemporary literature (van der Maarel and Franklin 2012, Thornton 2007) supports that there is a high probability that small, mainly herbaceous, fast-growing, short-lived species with extensive dispersal, allocating resources to reproduction (many, small and widely dispersible seeds, dispersed mainly by wind or birds, whose germination is induced by light) capable of growing with limited resources (mainly nitrogen), will dominate soon after a disturbance. On the other hand, late-successional plants species are larger, characterized by grow slow, with longer life span, allocating their resources to growth and structure (a few, big seeds, poorly dispersed mainly by gravity or mammals). Accordingly, traits such as life-form, growth form, Ellenberg's indicator values, seed production and weight, pollination type, and dispersal mode were used in this analysis. Our aim is to investigate (1) the temporal patterns of taxonomic and functional diversity since a previous eruption (alpha diversity), as well as of taxonomic and functional beta diversity, (2) the temporal patterns of individual traits used in the analysis, in order to provide more detailed information on species strategies at the initial and later stages of succession, and (3) the processes driving species assembly and whether they change over time since a previous eruption. Following the predominant theoretical framework, we postulate the hypothesis that volcanic eruptions act as a filter on the local species pool; thus, assemblages (i.e., censuses) right after the eruption would exhibit clustering of functional traits (according to the habitat filtering hypothesis). Over successional time, competition would play a more important role and might pose a limit to the similarity of coexisting species; thus, late-successional communities should become increasingly more functionally dispersed. Alternatively, according to the Mayfield and Levine (2010) theory, if increased competition results in the extinction of the least effective resource competitors, then functional clustering should remain stable or increase with time. This could be also the result in the case where assembly is driven first and foremost by environmental processes or environmental stress (Butterfield 2009). On a second level, we examined community-weighted mean trait values to distinguish the role of specific traits in the overall process and whether specific traits behave as theoretically expected.

METHODS

Study area

One of the oldest recorded cases of recovery of an island's ecosystem from devastation is that of the volcanic island of Santorini in the Aegean Sea, Greece (36°240′ N, 25°240′ E), although it has never been studied systematically (Vierhapper 1919, Raus 1988, Thornton 2007). Santorini archipelago is the most active center of the South Aegean Volcanic Arc (SAVA; also known as Hellenic Volcanic Arc), a chain of volcanic islands in the South Aegean Sea formed by plate tectonics as a consequence of the subduction of the African tectonic plate beneath the Eurasian plate (Druitt et al. 1999). The Aegean volcanic arc is one of the most important geological structures of the Mediterranean area. The arc stretches 450 km from the islands of Nisyros and Kos, through Santorini and Milos, to Peloponnesian Peninsula, and its width is no more than 20 km (Druitt et al. 1999). The long period of volcanic activities (more than 2000 yr) led to

the formation of two islands, Nea Kameni and Palea Kameni, representing the peaks of an intracaldera volcanic edifice, most of which is being under water. These islands together with Anak Krakatau (Indonesia) are two of the world's most prominent examples of marine emergent islands, unique and typical examples of primary Mediterranean and tropical succession, respectively (Whittaker et al. 1989, Thornton 2007). For more information on the study area, see Karadimou et al. (2015).

Nea Kameni (NK) emerged in 1570–73 and took its final shape after seven consecutive eruptive phases (Druitt et al. 1999). During the previous century, three eruptive phases took place on the island: in 1925–1928, in 1939–1941, and in 1950. As a result of the last eruption, in 1950, a part of the older surfaces were covered with fresh ashes (Raus 1988). At present, NK covers an area of 3.44 km^2 and reaches an altitude of 126 m. A map of the study area is presented in Fig. 1.

Floristic surveys on Nea Kameni

The first recorded floristic survey on NK was conducted about 40 yr after the vegetation-destroying eruptions in 1866–1870, in April 1911, when 84 vascular plant species were recorded (Vierhapper 1919). As the eruption of 1925–1928 had destroyed the plant cover completely (Raus 1988), Cammerloher, in his census in 1933, recorded only 24 species of higher plants, that is, less than one-third of the stock of 1911 (Cammerloher 1935). The partial
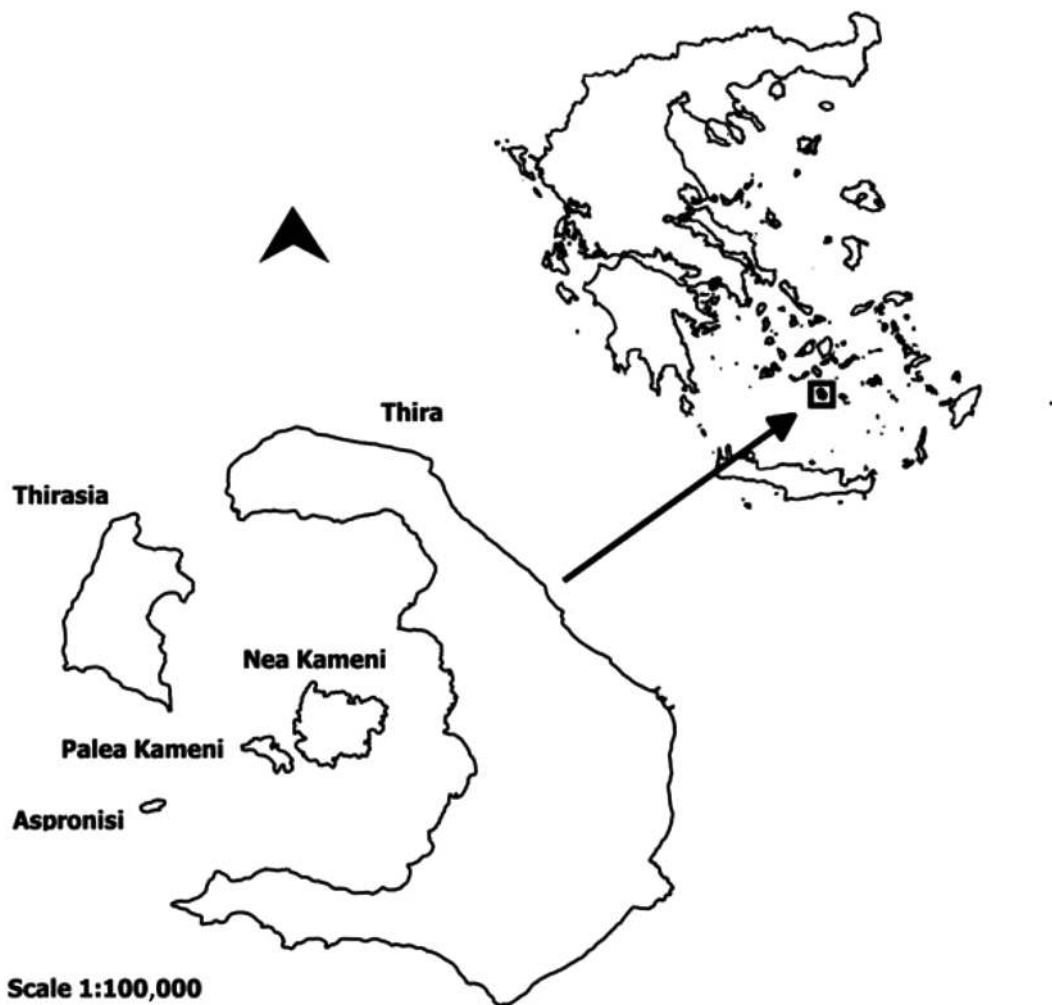

Fig. 1. General location and map of the Santorini archipelago with the intracaldera island of Nea Kameni.

destruction of the island's plant cover during the outbursts of 1939–1941 and 1950 was depicted in a census conducted in 1967 by Hansen (1971), collecting 84 species on NK: Among them, 26 new records, while 26 species mentioned by Vierhapper (Vierhapper 1919) and Cammerloher (Cammerloher 1935), were not found. T. Raus visited the island in 1984 and 1987 recording 119 and 133 species of vascular plants, respectively (published in Raus 1988). Thirty-three species in 1984 and 15 species in 1987 were new entries. In 2011, 100 yr after the first census on NK, T. Raus, P. Dimopoulos, I. Tsiripidis, E. Bergmeier, and E. Karadimou conducted a new floristic census, recording 139 plant species, with 25 species being recorded for the first time on NK. In this study, we analyze the floristic data (presence–absence data) recorded in 1911, 1933, 1967, 1984/1987 (these two censuses were unified to one due to their short time distance), and 2011, covering a period of 100 yr. In order to incorporate temporal patterns of diversity, we measure time in years between an eruptive event and the following census. Since there is no information about the reestablishment of vegetation on NK after the eruption of 1939–1941 and the extent of the impact of the 1939–1941's and 1950's eruptions on vegetation, we use the last eruption leading to a complete wipe out of vegetation on the island, thus the 1925–1928 eruption, as the point zero for the reestablishment of vegetation and for the calculation of the time intervals for each census. According to this methodology, the most extended time period of succession covered in this study is 83 yr. The nomenclature of species follows Dimopoulos

(2013). A timetable of the above events is presented in Fig. 2.

The 1866–1870 eruption led to the complete destruction of the vegetation on the island, like the eruption of 1925–1928 did. In the analysis, we include the time period from 1870 to 1911 as well. Despite the fact that the 1911 census is the only one that took place before the eruption of 1928 (an eruption that is regarded as time zero for the analysis) and represents a habitat type being lost and not recovered since, we have decided to include these data in the analysis for several reasons. First of all, we consider it important to include the species encountered on the island and recorded only at the 1911 census, because of the existence of a shore that it was destroyed in 1925–1928. Moreover, some of the species occurred in 1911 may have led to legacy effects on the vegetation after the eruption of 1928 which has proved to be a very important factor in succession.

Functional traits data

The first step in measuring functional diversity is to describe the functional strategies of species using a set of functional traits. The number of traits used in this study is large enough to sufficiently capture species functional uniqueness and small enough to avoid redundancy. We used a wide range of functional characteristics in order to incorporate interactions among species as well as species–environment relations. For each recorded taxon, 26 functional traits were collected that represent vegetative and regenerative characteristics as
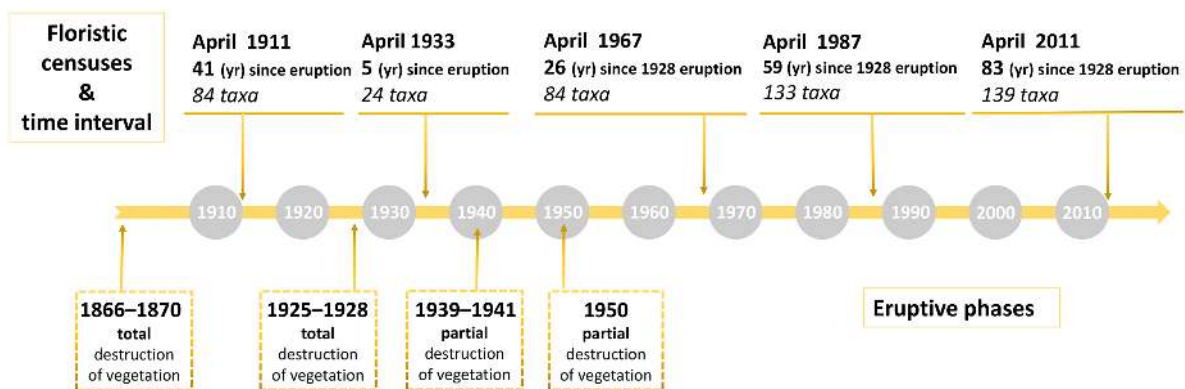

Fig. 2. Timeline of the eruptions on NK from 1866 to 1950 and the floristic censuses conducted from 1911 to 2011.

well as ecological preferences (based on Ellenberg's indicator values; Böhling et al. 2002) based on their ability to discriminate between early- and late-successional species according to their functional characteristics. They are related to the performance of species and represent different functional strategies for survival under particular environmental conditions. Moreover, a relatively high number of traits were used, based on the fact that the spatial pattern of the functional diversity is affected by the traits included in the calculation (Tsianou and Kallimanis 2016). Traits representing vegetative characteristics—mainly related to the competitive ability of species, growth, and disturbance tolerance—include longevity, maximum plant height, mean leaf length, mean leaf width, leaf length/width ratio, life-form, growth form, leaf surface texture, and canopy structure. The ecological preferences of plant taxa include indicator values for soil acidity, soil nutrient content, soil humidity, continentality, soil salt content, light, and temperature traits. Regenerative characteristics—related to species' dispersal ability in space and time—include flowering period start, flowering period end, flowering period length, seed production, seed weight, flower size, flower sex, pollination type, fruit type, and dispersal mode traits. For more detailed information, see Appendix S1: Table S1 and Karadimou et al. (2015).

Quantifying different facets of diversity

We calculated taxonomic (TD) and functional (FD) alpha (for each floristic census) and beta diversity (between each pair of floristic censuses) measures. We use species richness and Simpson's indexes to measure alpha TD, and 1—Jaccard index for beta TD (Koleff et al. 2003, calculated using the beta.pair function of the betapart package; Baselga and Orme 2012, in R; R Core Team 2017). We used two indices from the group of the multidimensional functional diversity indices group, which explore different facets of functional diversity to measure alpha FD: functional richness (FRic; Villéger et al. 2008) and functional dispersion (FDis; Laliberté and Legendre 2010). Two additional FD indices were used: Rao's quadratic entropy (RaoQ; de Bello et al. 2010) and functional dendrogram (Mouchet et al. 2010). These metrics were selected because they give the opportunity to quantify different facets of diversity using a common logic, the

multidimensional space, and have been widely used recently in the literature so that our results could be comparable.

These indices are designed to quantify functional diversity using continuous traits (Villéger et al. 2008). The traits' data used in this analysis include not only continuous variables (e.g., Ellenberg's indicators), but also qualitative functional traits (e.g., canopy structure) and circular traits (e.g., flowering period length). To deal with this complexity, as well as with the correlation among many traits, principal coordinates analysis (PCoA) was used according to Villéger et al. (2008) and Laliberté and Legendre (2010). Five ordination axes were retained (>90% of explained variation), and their scores were used as the new trait variables in order to calculate FD indices. The two indices as well as RaoQ were calculated using dbFD function of FD package (Laliberté et al. 2014), while functional dendrogram was calculated using the pd function of picante package (Kembel 2010) in R.

Beta FD was calculated using the framework introduced by Villéger et al. (2011) where functional dissimilarity (F_β) between assemblages is estimated by quantifying the dissimilarity in the functional space each of them occupy:

$$F_\beta = \frac{\text{Volume not shared}}{\text{Total volume}} = 1 - \frac{\text{Volume shared}}{\text{Total volume}}$$

Initially, the functional volume of each census was calculated (for 1911, 1933, 1967, 1987, and 2011 censuses). Then, the intersection of two functional spaces, for each pair of censuses, was calculated. Finally, the dissimilarity in the functional space between each pair was calculated using the above equation. This index is equivalent to Jaccard's dissimilarity index based on the number of species, and it was calculated using the functional.beta.pair function of the betapart package (Baselga and Orme 2012) in R.

All indices values were plotted against time (in years) since the previous eruption that destroyed completely the vegetation cover. Specifically, for the 1911 census, the previous massive eruption is that of 1870, while for the remaining four censuses the previous massive eruption is that of 1928. All analyses were conducted using the total list of taxa recorded but also the groups of the annual and perennial species separately.

Single-trait temporal changes using community-weighted mean (CWM) trait values

Temporal changes in single-trait values were estimated using community-weighted mean trait values in order to further comprehend changes in the strategies of species' assemblages with increasing time since an eruption and complement multivariate indices interpretation. The community (i.e., census)-weighted mean of trait values (Lavorel et al. 2008), that is, the functional composition of a set of communities, was measured by the community-level-weighted means of trait values (CWM), an index of functional composition, using dbFD function of FD package (Laliberté et al. 2014) in R.

CWM values were plotted against time (in years) since previous massive eruption. For the qualitative traits, the percentages of each trait's classes were calculated by dividing the number of species at each trait's class with the total number of species (for each census separately). Percentages were then plotted against time interval (in years) since previous eruption. Spearman's rank correlation coefficients and false discovery rate (FDR) threshold of 5% based on the method of Benjamini and Hochberg (1995) were used to assess the relationship between all diversity indices and time. Nevertheless, the small number of degrees of freedom (since we have available data from only five time points) is expected to decrease the power of test to detect statistically significant patterns; therefore, in this study we need to interpret the results with caution.

Statistical analysis on the assembly mechanisms

To investigate which mechanism drives community assembly, we used the modeling approach proposed by Mouchet et al. (2010). Initially, a randomization test was carried out comparing the values of each index calculated for each census with those of 999 random assemblages. To incorporate the correlation with sample size, the same method as Cornwell and Ackerly (2009) was used. Since the FD indices used are strongly related to species richness (Villéger et al. 2008, Mouchet et al. 2010), the comparison between observed and simulated FD values should refer to assemblages with the same number of species. Therefore, the indices values' comparisons were made between assemblages of the same species richness. The simulated assemblages were constructed using the total species list resulted from all five censuses. Hereafter, we estimated the rank position of each census among the highest or the lowest 50 random assemblages, according to their indices' values, assuming that ranking among the highest 50 positions (<0.05; greater functional richness [FRic] than expected by chance) indicates limiting similarity, while ranking among the lowest 50 (>0.95) positions (lower functional richness than expected by chance) indicates habitat filtering. All positions among those extremes indicate random processes.

RESULTS

Shifts in traits over time

CWMs (Appendix S3: Fig. S1) for the 26 plant functional traits did not display a clear trend with time since a previous eruption, with only few exceptions. According to Spearman's correlation coefficient, seed weight displays a strong statistically significant correlation with time; specifically, it decreases over time interval since previous eruption ($P < 0.05$) both for the total species' pool group and for the group of annual species, contrary to theoretical expectations. Other quantitative traits display a weaker correlation with time (Fig. 3; Appendix S1: Table S2), such as Ellenberg's indicator values for soil humidity that decreases for the total species' pool group and the flowering period end that progressively appears to start earlier in the year as well as Ellenberg's indicator value for light for the perennials. For qualitative traits (Fig. 4; Appendix S1: Table S3), the percentage of fruticose (i.e., having the form of a shrub) species decreases over time since eruption. Anemogamy species' (i.e., species dispersal of pollen by the wind) percentage decreases, while for hydrogamy (i.e., species dispersal of pollen by the water) it increases over time. The percentage of species with conspicuous flowers (Poaceae; thus categorized as having no flowers for the flower size trait) decreases, while the percentage of species with big flowers increases over time. The percentages of species with capsule, siliqua (and silicula), and spores fruit types increase over time. Results for statistically significant correlations of qualitative traits with time for the annual and perennial species groups are presented in Appendix S2: Figs. S1 and S2.
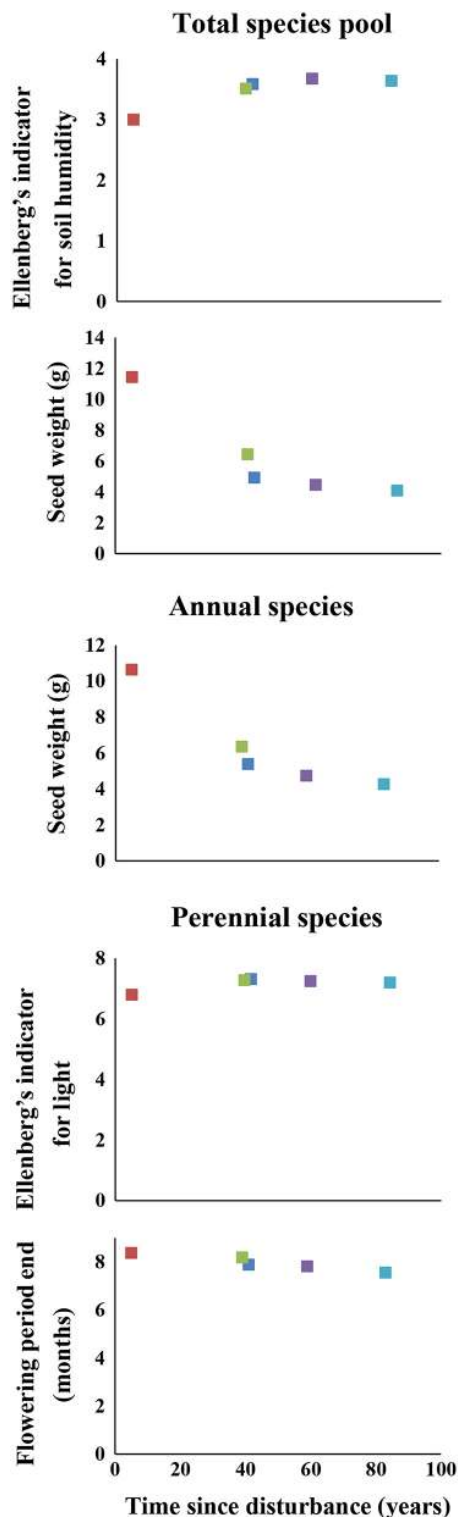
Fig. 3. Plots of the community-level mean values (CWMs), for three quantitative plant functional traits

Shifts in alpha and beta components of taxonomic and functional diversity over time

Results on changes in TD and FD over time since a previous eruption revealed that the components of diversity (taxonomic, functional) strongly dependent on species richness (represented in this study by species richness, functional richness, and functional dendrogram) increase with time, displaying similar temporal patterns (Fig. 5), and reach a peak after 59 yr since the eruption of 1928. Notably, the components of diversity that are independent of species richness and quantify the degree of dissimilarity between the members of a community (taxonomic or functional; represented in this study by Simpson's index, functional dispersion, and Rao's quadratic entropy) remain constant throughout the time period examined in this study (83 yr of succession). Plots of this second group of indices are displayed in Appendix S4: Fig. S1. Thus, as species richness and the volume of functional space increase over time, the average distance of individual species to the centroid of traits space (defined by the total species comprising the community) remains constant. Spearman's rank correlation coefficients between combinations of the three taxonomic and six functional diversity indices for the three species pools used in the analysis (total species pool, annuals species and perennial species separately) are presented in Appendix S6: Table S1.

Only taxonomic and not functional dissimilarity increases with increasing time between two censuses, indicating that assemblages closer in time are more similar in species' composition than more distant ones, but they do not differ functionally (Fig. 6).

(Fig. 3. *Continued*)

used in the analysis (out of a total of 26 traits), over time (in years) since an eruption. CWMs were calculated for the total species pool recorded at each of the five censuses (top two panels), as well as for annual and perennial species separately (middle panel and bottom two panels, respectively). Only statistically significant correlations according to Spearman's rank correlation coefficient are presented (see plots for all the traits analyzed in Appendix S3: Fig. S1). The five points represent the five censuses: red for 1933, green for 1967, purple for 1987, blue for 1911, and light blue for 2011 census.
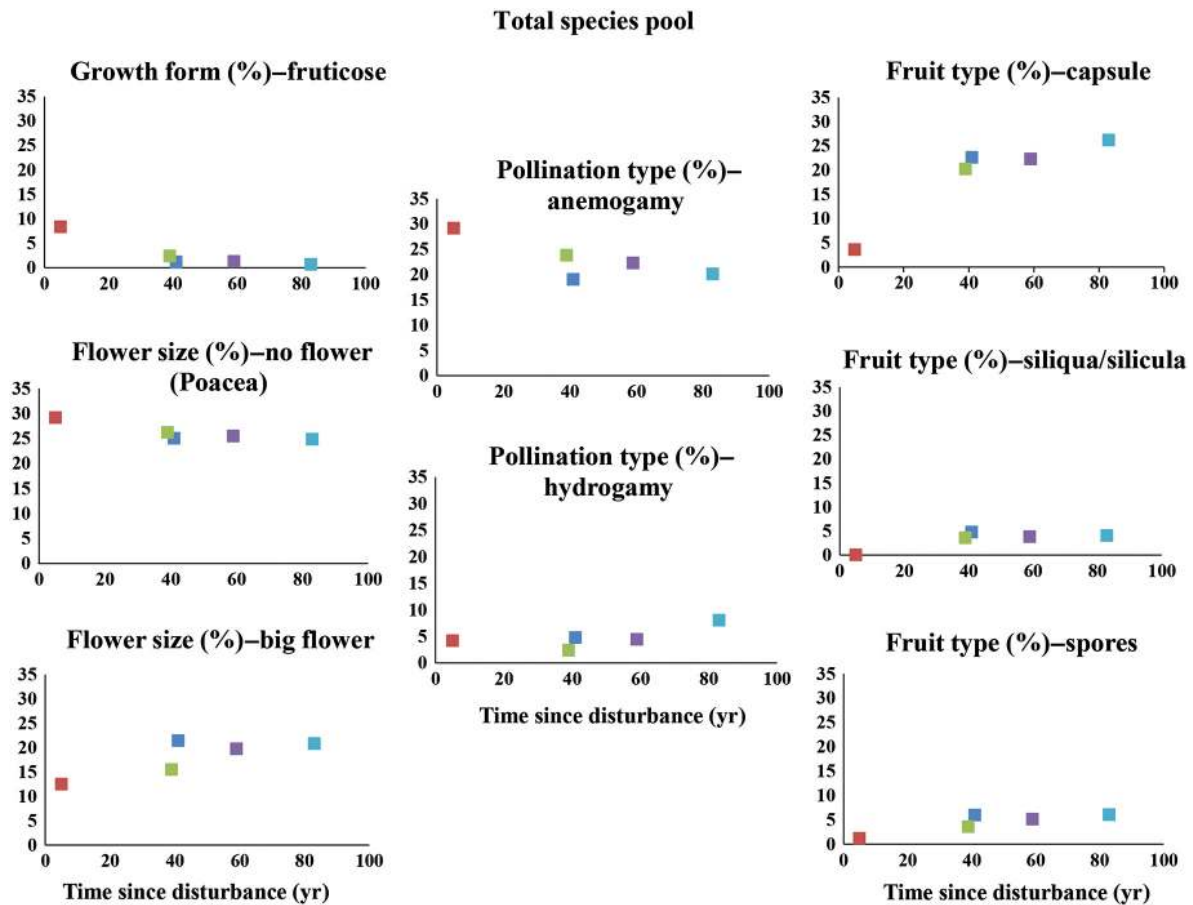
Fig. 4. Plots of the relative frequencies (calculated for the total species pool recorded at each of the five censuses) of the nine qualitative plant functional traits over time (in years) since an eruption. Only statistically significant correlations according to Spearman's rank correlation coefficient are presented (see all plots in Appendix S3: Fig. S2). Point colors like Fig. 2.

Long-term temporal changes in assembly processes

The analysis for the processes that drive species assembly did not reveal the theoretically expected pattern (a shift from habitat filtering toward limiting similarity over time; Fig. 7). Notably, the results display strong differentiation between the two FD indices used in the analysis. Functional richness, on the basis of the total species pool, strongly reveals the effect of habitat filtering in the species assembly process, at all time points except for the census conducted five years after an eruption (Fig. 7, first column, first row). On the contrary, functional dispersion indicates limiting similarity as the main driver of species assembly at both the shorter and longest time

periods after an eruption (Fig. 7, first column, second row). When analyzing annuals and perennials separately, the effect of habitat filtering (revealed by functional richness) becomes less strong on assemblages (Fig. 7, second and third column, first row), while limiting similarity effect (revealed by functional dispersion) becomes stronger on the assembly of annual species (Fig. 7, second column, second row) but also of perennials in three out of the four time points (Fig. 7, third column, second row).

Moreover, in order to understand which is the effect of the species' pool size (local or regional) used in the null model analysis on the species' assembly processes, we repeated the above analysis using the total species list recorded only on the
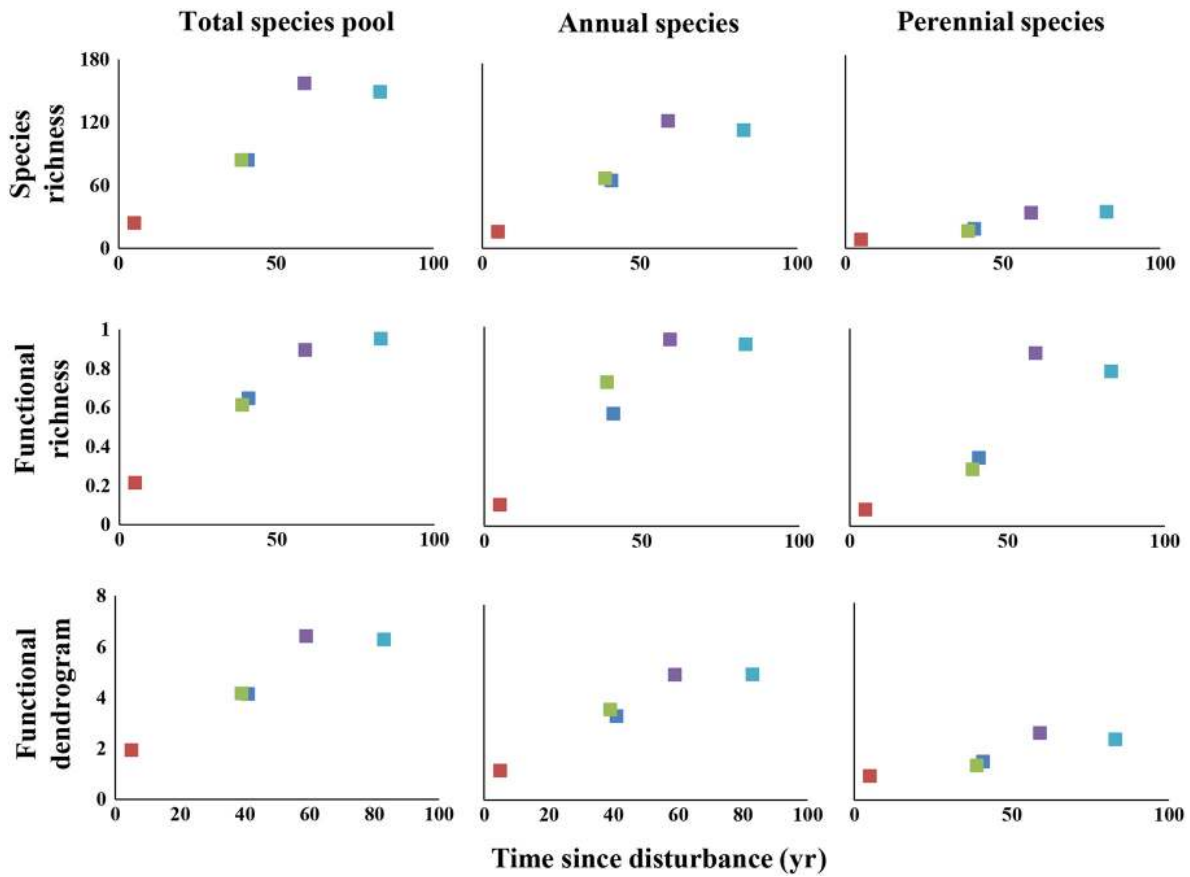
Fig. 5. Components of diversity (taxonomic, functional) strongly depend on species richness (species richness, functional richness, and functional dendrogram) over time (in years) since an eruption, for the total species pool recorded at each of the five censuses (first column), as well as for annual and perennial species separately (second column and third column, respectively). Point colors like Fig. 2.
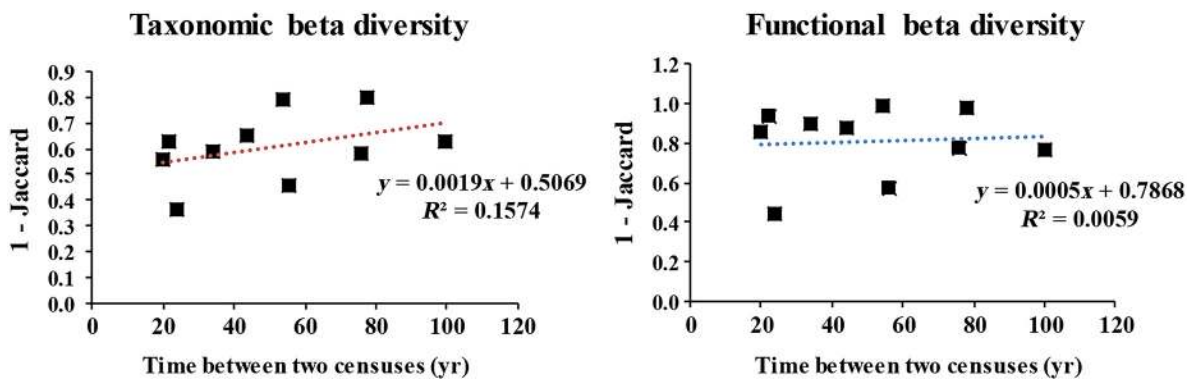

Fig. 6. Taxonomic and functional beta diversity indices' values based on 1-Jaccard index, for all possible pairs of censuses, plotted against time (in years) since an eruption, between each pair of censuses. Equation and R-square value for the linear model are presented on each chart.
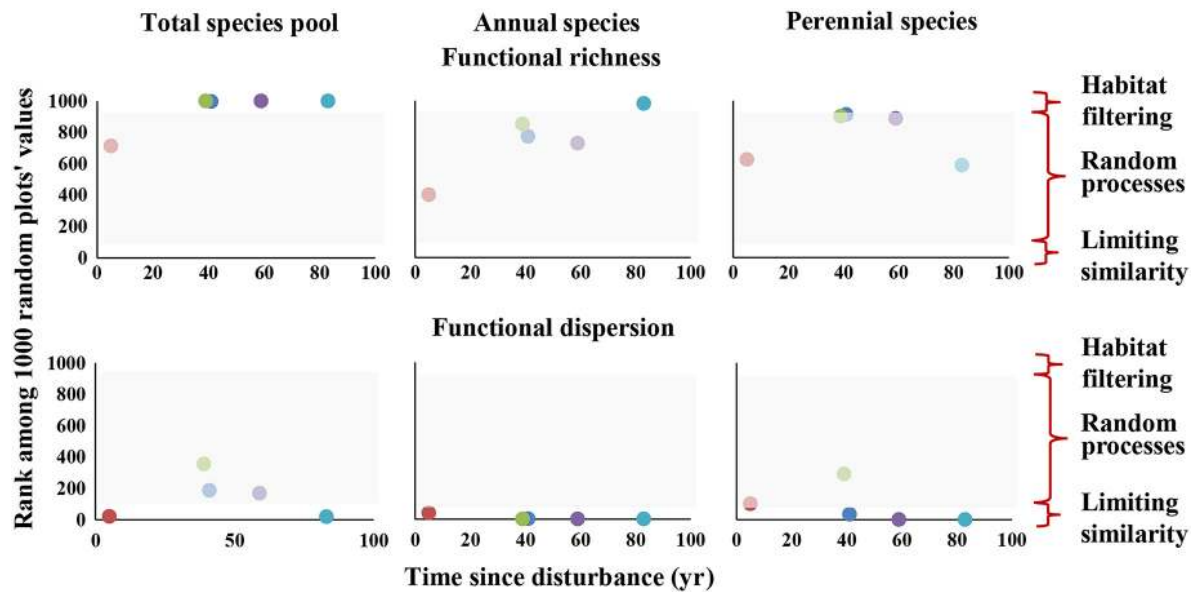
Fig. 7. Ranking of the FD indices' values (functional richness and functional dispersion) for the five successive censuses, among the values of 999 random assemblages. Ranking among the first 50 (1–50) positions indicates limiting similarity, while ranking among the last 50 (950–1000) positions indicates habitat filtering. For the creation of the random assemblages, the total species list of the archipelagos was used (regional species pool). Point colors like Fig. 3.

NK island from 1911 to 2011. The analysis revealed that mainly stochastic events shape the assemblage of NK's flora over time since eruption and only in a few cases limiting similarity, mainly, appears to affect communities' assembly at various time points after the disturbance as depicted by both functional richness and functional dispersion indices. The results are displayed in further detail in Appendix S5: Figure S1.

DISCUSSION

Temporal changes in different diversity facets

In our study, we demonstrate long-term temporal changes in functional trait composition and functional diversity as well as in the factors driving community assembly following eruptions over the last 100 yr on the Mediterranean volcanic island of Nea Kameni. Some of our results are in accordance with the classic theoretical framework on succession, while, interestingly, the majority of our results support the role of more recently proposed factors that pose a strong influence on succession, such as legacy effects.

As expected, total taxonomic and functional richness increase over time after previous eruptions. Nevertheless, by incorporating other facets of functional diversity in our analysis, we found that not all diversity facets display the same increasing pattern over time. Our results indicate that while taxonomic and functional richness increase with time, functional dispersion remains constant. This results is opposite to the classical theoretical expectations that early-successional species would be pioneer species sharing a suit of traits (Cornwell et al. 2006, i.e., small, mainly herbaceous, fast-growing, short-lived species with extensive dispersal, with many, small and widely dispersible seeds, dispersed mainly by wind or birds, whose germination is induced by light, capable of growing with limited resources). The fact that functional dispersion reveals high value of functional dissimilarity even among the first pioneers may be attributed to the presence of species that persisted on the island during the volcanic eruption and managed to tolerate the severe disturbance (e.g., by persisting in the soil seed bank or through the survival of underground plant parts). Moreover, since the distance

of NK to the nearest island species pool is very short, this result might reflect a relatively high degree of randomness in the arrival of the pioneers with many perennial species among them, since it has been reported in previous studies that shrub species are among pioneers on rocky substrates (Diamond 1975, Whittaker 1992, Thornton 2007). The proximity of the nearest islands along with the depositions of ashes during the last eruption that provide a more fertile substrate than lava blocks allowed species of different traits to establish. Indeed, taxa recorded five years after the eruption of 1925–1928, such as *Asparagus horridus, Avena barbata, Crepis multiflora, Ficus carica, Helichrysum italicum, Lupinus angustifolius, Rumex bucephalophorus* subsp. *aegaeus,* and *Solanum nigrum* subsp. *nigrum,* are very dissimilar regarding most of their functional traits. Similar findings have been reported following the volcanic eruptions and subsequent community assembly of Mt. St. Helens (Chang and HilleRisLambers 2016). This is also supported by the high percentage of perennial species in the new assemblage, five years after the eruption of 1939–1941, that was not expected since the eruptions of 1925–1928 resulted in the complete devastation of vegetation on the island (according to the findings of Cammerloher 1935). As time passes, the majority of pioneer species establishing on the island are annuals, according to theoretical expectations on the initial stages of succession. According to Meiners et al. (2015*b*), succession events are a result of the interaction among three major parameters: the differential site availability, the differential species availability, and the differential species performance. Site availability derives not only from the severity of the disturbance event but also from factors like spatial pattern and timing. Andersen and MacMahon (1985) have reported that the single event of the 1980 eruption on Mt. St. Helens produced a great variety of substrates (mud and ash flows, wide deposits of ash, and coarser airborne debris) on which subsequent vegetation dynamics were differentiated. Although there were many sites in which all adult plants and seeds were killed, there were patches in some sites, such as the pumice plains, in which fast-growing nitrogen fixers emerged from a surviving seed source.

Our results suggest a strong legacy effect in vegetation development. Many studies (on volcanic substrata as well) support that knowledge of past disturbance history can provide necessary context for understanding legacy effects on succession (among others: Tsuyuzaki and Moral 1995, Walker and Wardle 2014). Subterranean storage parts of plants (rhizomes, tubers) have survived buried under ash to depths of more than 30 cm (Thornton 2007). Whittaker et al. (1995) found plants germinated from seeds located in ash-buried soil for several years by several centimeters of ash on Anak Krakatau, while propagules' growth has been reported for Mt. St. Helens (Antos and Zobel 2005). Notably, Dimopoulos et al. (2010) have reported that the distribution of ashes after the recent volcanic eruptions controls the formation of local pioneer vegetation on NK. This fact could explain the pattern of functional dispersion over time, while, at the same time, the colonization of the island by new species increases the functional space, indicating the strong correlation between functional richness and species richness.

The strong legacy effect is also supported by the temporal beta diversity. While taxonomic beta diversity increases when assemblages are more distant in time, functional beta diversity remains constant indicating probably functional redundancy (contrary to theoretical expectations according to which functional redundancy increases over time leading to functional homogenization; Sonnier et al. 2012, Villéger et al. 2014). The above results highlight the importance of legacy effects on succession, since the prevalence in early succession stages of species belonging to later stages decreases species replacement rate and leads to more similar vegetation types at nearby or similar ecosystems (Walker and Del Moral 2003).

Temporal changes in species strategies

The majority of traits did not display statistically significant changes over time since eruption as expected by succession theory for primary succession (Connell and Slatyer 1977, Weiher and Keddy 1995), a result that further supports legacy effects. However, some traits displayed changes in accordance with the theoretical framework (reduction in anemochory species, reduction in Poaceae species, increase in species with big flowers) indicating the transition from pioneer species to later colonists. Pioneers of the

early stages of primary succession often fit the r-selected strategy, although invasion can come from local, mature, K-selected vegetation where initial conditions are severe or the potential flora is limited (Walker and Del Moral 2003). In our case, assemblages in the first years after the eruption had greater wind dispersal ability and lower growth rate (for the annuals species group) and disturbance tolerance than assemblages later in succession. The presence in NK of these species, among them *Lupinus angustifolius*, alters soil nutrients, the light regime, and opportunities for colonization, facilitating the arrival of later colonists by altering the biotic and abiotic environment (by increasing moisture holding capacity and temperature, as well as soil stabilization with higher percentage of grasses among them, and soil nutrient enrichment).

Contrary to theoretical predictions on temporal changes in community trait composition between early- and late-successional colonists, we found that late colonists have lower mean seed weight and are well adapted in high-drought conditions, including species with bigger, entomogamy or autogamy flowers. Seed bank and/or plants' survival after the eruption change the initial stages of succession compared to theoretical expectations of primary succession. According to these results, assemblages later in succession on NK reflect the effect of the harsh environmental conditions where pioneer species coexist with late colonists and facilitation on both directions is necessary for the survival of species without clear evidence of a direction toward other stable stages of succession.

Changes in species assembly over time since eruption: the effect of environmental stress and facilitation

Recently, long-term succession studies have begun to test hypotheses on which stochastic and/or deterministic processes are more important in early versus late succession by applying recently introduced analytical tools developed in the community assembly literature (see a review in Meiners et al. 2015*b*). Several studies (among others: Purschke et al. 2013, Marcilio-Silva et al. 2016) support the general framework indicating that dispersal generally plays the strongest role immediately following a disturbance, while abiotic factors are thought to play a strong role early

in succession and biotic interactions (first facilitation and then competition) become increasingly more important as succession progresses. Our results come in accordance with studies emphasizing on the importance of priority effects (Fukami 2015), legacy effects (Swanson et al. 2011), and other stochastic processes such as rare events (e.g., climate extremes) that have the potential to alter community trajectories (Chase 2007, Zhou et al. 2014). Such factors must be regarded as a supplement to the above theoretical framework, and they should not be neglected in succession predictions.

Moreover, different facets of functional diversity reflect more than one process acting at the same time. Functional richness suggests that pioneer species assembly during primary succession is driven initially by stochastic events, a result that comes in accordance with theoretical expectations. Nevertheless, at the same time, functional dispersion revealed high dispersion of traits in the primary assemblage (only five years after the eruption of 1925–1928) indicating limiting similarity. This result probably reveals the intense competition that the high proportion of perennials in this primary assemblage influences the rest of the species (annuals). Notably, these perennial species persist during succession on NK. It has been reported that when conditions initially allow the colonization and expansion of woody species, prevalence of the propagule pool by a species will likely result in the prevalence by these species, at least temporary (Helsen et al. 2012). An additional level of complexity may be detected when the timing of seeds arrival influences community composition and develops long-lasting priority effects (Helsen et al. 2012). It is also possible that the prevalence of N-fixer *Lupinus angustifolius* at this stage of succession inhibits colonization or growth of other annuals, due to its ability to dominate resources (Shainsky and Radosevich 1992).

As time passes, community assembly is driven mainly by deterministic processes, that is, habitat filtering, according to functional richness, and this mechanism continues to persist and dominate community assembly throughout the time period examined (83 yr after a volcanic eruption), contrary to theoretical predictions on biotic interactions predominance as succession proceeds (Callaway and Walker 1997). This

highlights the importance of the harsh environmental conditions (extreme drought) on the island, which result in the establishment only of species that can tolerate the physical conditions of the environment. For the same time period, functional dispersion component indicates that other processes may also play an important role in community assembly. A few years after the eruption, stochastic events are revealed, while after longer time periods, over-dispersion of traits characterizes species assembly. This component is linked to the random arrival of new colonizers, occupying space left open by pioneer species, for example, more fertile soils created on areas where *L. angustifolius* was formerly abundant. Eighty-three years after an eruption, functional dispersion highlights the role of biotic interactions in community assembly. When harsh environmental conditions predominate, tolerance and not competition is initially detected to dominate biotic interactions among species, since facilitation often allows coexistence in stressful environments while a longer time period is needed for the first species to increase resource availability and competition to become evident (Butterfield 2009). Since facilitative interactions involve functionally distinct species (Callaway 2007), facilitation could act to prevent coexisting species from being too similar and increase functional diversity in stressful environments. Competition might also be present in late stages of succession, since multiple shifts between facilitation and competition may occur during succession, depending on the life stage of the facilitated species but also on spatiotemporal fluctuations in the environment. The balance tends to be positive if niche of the adult stage of the facilitated plant overlaps with that of its nurse and negative if both niches tend to differentiate (Soliveres et al. 2010).

Additionally, we found a clear effect of the species' pool size (local or regional) on the species assembly processes that each index indicates. When the total archipelagic species pool was used (regarding functional richness component), a stronger effect of habitat filtering was revealed compared to the results produced using the local species pool (as analyzed above). This finding supports that at coarser spatial scales, habitat effects will be detected (Weiher and Keddy 1995, Santos et al. 2016).

The analysis of annual and perennial species separately indicates that the assembly of annuals is mainly characterized by random arrival and competition among individual species in the attempt to colonize the island, while habitat filtering is the main driver only at the final stage of the analysis. Assembly of perennials, on the other hand, is driven by habitat filtering early in succession, while as time passes, limiting similarity plays a more critical role. Observations on the island of NK regarding other shrub species (with only one or two individuals) indicate that their failure to spread may be attributed to the combination of limited resource availability and intense competition exerted by already established scrub species.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2374/full