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RESEARCH ARTICLE

The spatiotemporal distribution of pollen traits related to dispersal and desiccation tolerance in Canarian laurel forest

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Abstract

Questions: Pollen traits (e.g., size, wall thickness, number of apertures) have been suggested to be relevant in terms of pollination mechanisms and the ability of the male gametophyte to withstand desiccation. We examined the spatiotemporal distribution of pollen traits related to dispersal (ornamentation and dispersal unit) and desiccation tolerance (wall thickness, presence of furrows and pores and pollen size). Specifically, we address two questions: how are the pollen traits distributed in relation to different levels of aridity? And, how did the pollen trait composition change with changing past environmental conditions?

Location: Laurel forests of La Gomera and Tenerife (Canary Islands).

Methods: We used pollen rain from 19 forest plots on an elevational gradient of 1050 m and all laurel forest types (cold, dry, humid and ridge crest) to quantify pollen trait composition using community-weighted means. In addition, we used fossil pollen to examine the composition of pollen traits over 9600 years in response to known intervals of regional past climate change.

Results: Our results demonstrated increased prevalence of desiccation tolerance-related pollen traits over drier areas of the laurel forest distribution. We also found increased prevalence of rich pollen grain ornamentation in the core of the laurel forest distribution. Holocene pollen functional diversity increased during a trend towards drier conditions as did the proportion of pollen grains with apertures and thicker walls to indicate desiccation tolerance.

Conclusions: Our study provides the first step towards understanding the role of pollen traits when quantifying the dynamics of different plant communities.

KEYWORDS

Canary Islands, Holocene, laurel forest, palaeoecology, pollen traits

1 | INTRODUCTION

Identifying plant traits that enable plant species to cope with environmental change has been highlighted as an important research goal (Aguirre-Gutiérrez et al., 2022). It allows assessing how plant communities respond to shifts in climate and to identify those plants that might be more resilient to past, current and future environmental change (Díaz et al., 2016; Kühn et al., 2021). However, pollen traits have been largely overlooked. Our paper contributes to this research through the analysis of pollen morphological traits related to desiccation tolerance and dispersal from laurel forest trees and shrubs on the islands of La Gomera and Tenerife, Canary Islands (Figure 1). The overall aim of the paper is to shed new light on how the distribution of pollen dispersal and desiccation traits vary over space in the Canarian laurel forest and through time using palaeoecologic records.

Viable pollen grains are important for plant dispersal and fitness (Dafni & Firmage, 2000). It has been suggested that specific pollen traits might be significant for plant fitness (Franchi et al., 2011; Pacini & Hesse, 2012; Abrego et al., 2017; Seddon et al., 2021). In particular, changes in the moisture level may differentially affect the viability of pollen with high and low desiccation tolerance, which finally impacts plant dynamics and survival (e.g., Franchi et al., 2011). For example, thin pollen walls have been documented for taxa living in environments of high relative humidity as thinner pollen walls provide an advantage in terms of more rapid germination due to shorter rehydration times (Osborn et al., 2001; Pacini & Hesse, 2012). Another example is the relationship between the number of apertures (e.g. furrows and pores) and desiccation tolerance (Franchi et al., 2011). In pollen grains with low desiccation tolerance (recalcitrance), furrows are absent and there may be an absence of pores too (Franchi et al., 2011). The absence of apertures prevents the loss of water from the pollen grain, enabling immediate germination if moisture becomes available (Franchi et al., 2011). On the contrary, pollen grains with high desiccation tolerance (orthodoxy) present furrows that allow changes in pollen volume during dehydratation and rehydration phases (Tweddle et al., 2003). In addition, a thicker pollen wall and larger pollen size with a lower surface-to-volume ratio are thought to protect the grain from desiccation and are suggested to be prevalent in the forest edges, where ultraviolet (UV) light is more intense and environmental conditions are harsher (Pacini & Franchi, 1999; Ejsmond et al., 2011; Norros et al., 2015). We are also interested in analysing the relationship between the variation in the exine sculpturing, pollen size and shape and the dispersal mode. However, this relationship is a subject of debate and a source of uncertainty (Vaknin et al., 2000; Norros et al., 2015; Abrego et al., 2017). There is some evidence of a relationship between rich ornamentation and entomophily, as it is thought that ornamentation plays an important role in the attachment to insects and to the stigma of the flower, but see Hesse et al. (2000) and Konzmann et al. (2019) for further discussion. Pollen grains of wind-pollinated species often lack elaborate sculptures and appear smooth (i.e., psilate) and/or they have sac-like attachments (saccate) to help in their transport through the air (e.g., *Pinus* and many other coniferous species) (Linder, 2000; Williams, 2010).

Finally, we apply the pollen trait approach to palaeoecological data sets as a new aspect in the reconstruction of past vegetation dynamics. The change recorded in the laurel forest communities was hypothesized to be related to a regional climatic shift towards drier conditions (de Menocal et al., 2000; Kröpelin et al., 2008; Nogué et al., 2013). Whereas changes in the forest community from La Gomera were related to the increasing drier condition during the end of the African Humid Period (Nogué et al., 2013), the Tenerife core covered only the last 4700 calibrated years before the present (cal.

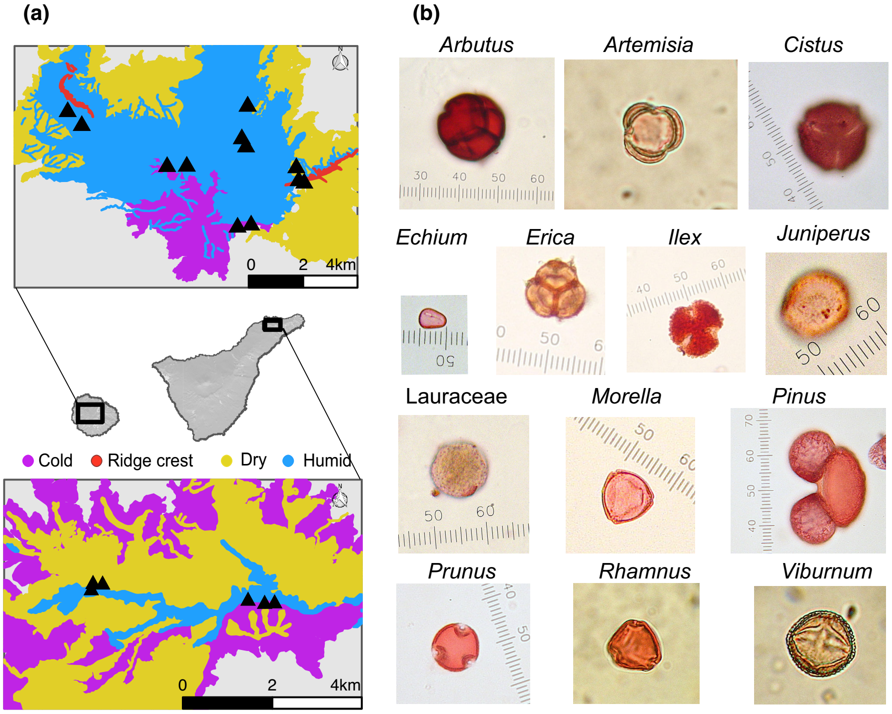

FIGURE 1 (a) Location of study sites in Tenerife and La Gomera (black triangles) in the four types (dry, humid, cold and ridge crest) of laurel forest (after del Arco Aguilar et al., 2010). Tenerife study sites from de Nascimento et al. (2015). (b) Examples of the morphology of some pollen grains included in the study sites. Scales on the pollen pictures are in μm. Pictures: Lea de Nascimento and Sandra Nogué.

year BP), during which a slight trend towards more mesic conditions began around 2900 cal. Year BP, followed by more dramatic changes after human colonisation around 2000 cal. year BP (de Nascimento et al., 2009). The fossil pollen data sets from La Gomera showed that plant communities commenced a relative shift from hygrophilous taxa (*Phoenix* and *Salix*) to greater dominance of the xerophilous *Morella–Erica* heath at around 5000 cal. year BP (Nogué et al., 2013). Here, we assess whether past regional intervals of drought were reflected in the profile of pollen traits by an increase in desiccation tolerance pollen traits.

We aim to examine patterns of pollen morphological traits related to desiccation tolerance and dispersal in the Canarian laurel forest to examine the spatiotemporal distribution of pollen traits. Specifically, we address two research questions:

1. How are the pollen traits distributed across study sites? We hypothesise that plant communities growing in drier environments would have a higher preponderance of species that have pollen traits associated with desiccation tolerance. We also hypothesise that pollen dispersal traits would follow a gradient across laurel forest types.
2. How did the pollen trait composition change with changing past environmental conditions? We hypothesise that past regional intervals of drought were reflected in the profile of pollen traits.

2 | METHODOLOGY

2.1 | Study sites

For the modern pollen part, we studied 13 sites in Garajonay National Park on La Gomera and six in Anaga Rural Park on Tenerife from de Nascimento et al. (2015) (Figure 1; Appendix S4). We followed the del Arco Aguilar et al. (2010) laurel forest classification that largely describes the distribution by elevation band (dry: 450–800 m a.s.l.; humid: 800–1250 m a.s.l.; on ridge crests area: both below and above 1100 m a.s.l.; and cold: 1250–1500 m a.s.l.) (see also Fernández-Palacios et al., 2019). The 19 study sites, which represent the four forest types listed above, are coded as follows (Appendix S4): EM and MA representing Tenerife sites and all others representing sites from La Gomera:

1. Dry laurel forest (APO, MA1-3, SEC): windward forest communities dominated by *Apollonias barbujana*, *Arbutus canariensis*, together with *Erica arborea*, *Ilex canariensis and Morella faya*.
2. Humid laurel forest (ACE, ATA, ATB, BAI, EM1-3, JOR, OCO, PAL, TAJ): here accumulations of clouds from 840 to 1560 m a.s.l. control the species composition and structure (Fernández-Palacios et al., 1995; Fernández-Palacios et al., 2019) of the forest community, which is dominated by 20–30 m tall trees, including *Apollonias barbujana*, *Erica arborea*, *Ilex perado*, *Laurus novocanariensis*, *Morella faya*, *Prunus lusitanica and Rhamnus glandulosa* and two shrub species, *Sambucus nigra* ssp. *palmensis* and *Viburnum rigidum*.
3. Cold laurel forest (FAY, NOR, TAJ): located at 1250–1500 m a.s.l. and dominated by *Morella faya*, *Erica arborea*, *Ilex canariensis* and *Laurus novocanariensis* (Fernández-Palacios et al., 2019).
4. Ridge crest forest (ARA, BAI): distributed along crests and ridges around 1100 m a.s.l. The most frequently occurring arboreal species are *Erica platycodon*, *Ilex canariensis*, *Laurus novocanariensis*, *Morella faya*, *Prunus lusitanica and Viburnum rigidum* (Fernández-Palacios et al., 2019). Depending on the classification ARA could be considered humid laurel forest and TAJ, ridge crest forest.

2.2 | Laurel forest pollen rain collection

The pollen rain was collected from the 13 study sites in Garajonay National Park to supplement the data collected from the six study sites from the Anaga Rural Park by de Nascimento et al. (2015). The pollen traps, based on the design of Behling et al. (2001), comprised 100-cm^3 plastic tubes with an aperture of 4.2 cm in diameter, filled with 10 ml of glycerine and covered with 1-mm gauge nylon mesh and fixed to an iron bar inserted in the ground so that the trap was positioned 10 cm above the ground surface. Following the experimental approach used by de Nascimento et al. (2015) four pollen traps were placed in the centre of each of the 13 study sites ($N = 52$). These complemented the 24 previously collected pollen traps from the six study sites from Anaga Rural Park (de Nascimento et al., 2015). They remained in situ from November 2013 to December 2014. The forest composition was recorded for a standard plot size of 2500 m^2 (50 m × 50 m) around the pollen trap sites. Some plots were smaller due to site orography (Appendix S4).

2.3 | Pollen identification and quantification

A known quantity of spores of the exotic clubmoss *Lycopodium* spp. was added to pollen samples as a quantitative marker, before samples were passed through a 150-µm sieve to remove plant material, treated for 1 min with an acetolysis mixture involving acetic anhydride and sulphuric acid in a ratio of 9:1, dyed with safranin and dehydrated using tert-butyl alcohol. Pollen samples were mounted on slides in silicone oil (Bennett & Willis, 2001). We counted a minimum of 100 pollen grains from each of the four pollen traps. Identification was based on the reference pollen collection held at the University of Oxford Long-term Ecology Laboratory and the Global Pollen Project (Martin & Harvey, 2017).

2.4 | Pollen traits

We recorded seven pollen traits (Appendix S6), comprising: pollen size measured as longer axis (large: 51–100 µm; medium: 26–50 µm, small: 10–25 µm); exine or wall ornamentation (simple: psilate, foveolate; moderate: rugulate, reticulate, striate; complex: baculate, clavate, echinate, gemmate, granulate, heterobrochate, scabrate, verrucate); dispersal unit (monad, saccate, tetrad); pollen shape (oblate, prolate, spherical); presence of furrows (0, 1, 2, 3, >3); presence of pores (0, 1, 2, 3, >3); and pollen wall thickness (thin: <1 µm; thick: >1 µm). In addition to laboratory-based measurements, trait data for the taxa present were also derived from the Global Pollen Project (Martin & Harvey, 2017) and the Palynological Database-PalDat (https://paldat.org; data retrieved in January 2020).

2.5 | Statistical analysis

2.5.1 | Pollen rain composition

For each sampled study site, we analysed 21 pollen taxa of trees and shrubs. We identified the pollen taxa at least at genus level with the exception of Lauraceae that was included at family level (see Appendix S5,S6). In each sample, we calculated for each taxon the pollen percentage of total pollen in the sample. Note that although *Pinus canariensis* is not present in the laurel forest study sites, *Pinus* pollen was included in the analyses due to the presence of pollen grains in our modern pollen survey. *Pinus canariensis* is abundant on Tenerife, but less so on La Gomera, where there is currently no pine zone habitat above the laurel forest (del Arco Aguilar et al., 2010).

2.5.2 | Pollen trait community-weighted means

For each of the 19 study sites, we calculated the community-weighted mean (CWM) for each pollen trait (Lavorel et al., 2008). For the furrows and pores traits, this was calculated as the mean trait value for all taxa in the community. For categorical traits (dispersal unit, pollen size, pollen shape, ornamentation and wall thickness), this was calculated as the abundance of each individual class, varying between 0 (low abundance) and 1 (high abundance) for a trait. We log-ratio-transformed the CWM plotting for those traits which are categorical (all except number of furrows and pores). We used for the calculations the 'functcomp' function from the *FD* package in R (Laliberté et al., 2014).

2.5.3 | Holocene changes in pollen traits and functional trait space

To understand how pollen traits changed through time, we calculated: (1) the proportion of pollen traits over time for the taxa included in this study (Appendix S5); and (2) functional dispersion at each point in time. To ensure that taxa appearing through time were included in these data, we complemented our modern data sets with pollen taxa from the fossil pollen data sets. These included for example *Carpinus*, *Quercus*, *Phoenix canariensis*, *Sambucus nigra* spp. *palmensis* and *Salix canariensis* (Appendix S5,S6).

First, we used fossil pollen data from two sites, La Laguna (28°30′ N, 16°19′ W; 560 m a.s.l.) on Tenerife covering the past 4700 cal. years, and Laguna Grande in Garajonay National Park, close to the highest point of La Gomera (28°07′ N, 17°15′ W; 1250 m a.s.l.) (Nogué et al., 2013), covering the past 9600 cal. years. The latter site is located within 200 m of the FAY cold laurel forest site (1266 m a.s.l.; Appendix S4). We calculated the proportion of pollen traits over time for the taxa included in this study and we compared the trends with regional palaeoclimatic data. The palaeoclimatic data are based on the quantitative reconstruction of western Saharan precipitation derived from leaf wax isotopes from marine core GC37 (Tierney et al., 2017) and marine core GC27 for the reconstruction of the aeolian dust providing a record of past changes in atmospheric circulation and aridity (McGee et al., 2013a; McGee et al., 2013b) (Appendix S3). Second, to calculate functional dispersion as a characteristic of pollen traits, we first determined the different palaeoecological pollen communities for each time point (number of time points = 37 for La Gomera and 28 for Tenerife). We then used the 'dbFD' function of the *FD*package in R to calculate the functional dispersion of communities (Laliberté et al., 2014). For both analyses we used generalized additive models (GAMs) using the package *mgcv* in R (Wood, 2022).

3 | RESULTS

3.1 | Pollen rain composition

The number of pollen grains per pollen trap in La Gomera ranged from 252 (ACE, humid laurel forest) to 781 (SEC, dry laurel forest) (Appendix S1,S4). The best represented pollen taxa were *Morella* and *Erica*. The relative abundance of Lauraceae was generally low but it was present in all study sites, ranging from 0.1% (SEC) to 1% (NOR, cold laurel forest), consistent with the known low pollen production dispersibility of these entomophilous species (Appendix S6, Figure S1). Pollen composition and abundance varied between laurel forest sites in Garajonay National Park. For example, two dry laurel forest sites, SEC and APO, were dominated by *Morella* trees, reaching 85% of the total pollen composition. ATA, ATB and JOR (humid laurel forest) and FAY (cold laurel forest) featured generally high levels of tree pollen from *Morella* (50 to 60%), with a contribution of *Erica* (10 to 30%) and *Ilex* (<10%). The most common pollen types of ACE, BAI (humid laurel forest), NOR and TAJ (cold laurel forest) were *Erica* and *Morella*, followed by *Ilex* and Lauraceae. Although pollen from *Erica* and *Morella* have been recorded in ARA (ridge crest) and OCO (humid laurel forest), the sum of both taxa accounted for <40%. However, both sites presented high levels of *Ilex*, 20% and 40%, respectively. PAL (humid laurel forest) site featured a high percentage of *Erica* pollen (44%) and a low percentage of *Morella* pollen (17%) (Appendix S1).

3.2 | Pollen trait community-weighted means

Pollen taxa with more furrows and pores were more prevalent in dry laurel forest sites than in humid, crest and cold forests (Figure 2). Both pollen taxa with simple and complex ornamentations were better represented than moderate ones. Overall, pollen taxa of medium and small size were better represented than pollen of larger sizes. The highest prevalence of medium-sized pollen grains was found in the dry laurel forest sites. A larger proportion of small pollen was found in the humid laurel forest and of larger pollen in the cold laurel forest. Across study sites, pollen taxa with thicker pollen walls were better represented than those with thin pollen walls. However, the ratio of thick to thin pollen walls declined from dry forest sites to ridge crest, humid and cold. Pollen taxa dispersing as monads were the best represented for all forest types, with bisaccate pollen was the least represented. Finally, in all site types, most pollen taxa were spheroidal and there were no differences between laurel forest types (Figure 2).

3.3 | Holocene change of pollen traits focusing on desiccation tolerance

When looking at the distribution of different pollen traits through time, we found that the proportion of pollen grains with apertures increased towards the present. In addition, pollen grains with thicker walls increased towards the present for La Gomera, but in Tenerife remained stable (Figure 3a–c). For the La Gomera pollen record these changes occurred during a time interval for which palaeoclimatic data suggested that the regional climate became drier at around 5500 years ago (Figure 3e, Appendix S3). In addition, we also found that for the La Gomera palaeoecological record, pollen functional trait space was greater from 5000 cal. year BP to the present than in the previous period. From 9600 cal. year BP to the present, levels of functional dispersion fluctuated from values of around 0.20 to 0.35. From 7500 to 5000 cal. year BP, there was an increasing trend to values of around 0.35, followed by a small decline towards the present (Figure 3d). The Tenerife palaeoecological record that started at 4700 cal. year BP displayed a similar declining trend towards the present. The change in the precipitation proxy from marine core GC37 had already taken place at the point when the Tenerife pollen record begins (Tierney et al., 2017). There is no evidence suggesting precipitation-driven changes in the laurel forest at La Laguna during 4700–4200 cal. year BP.

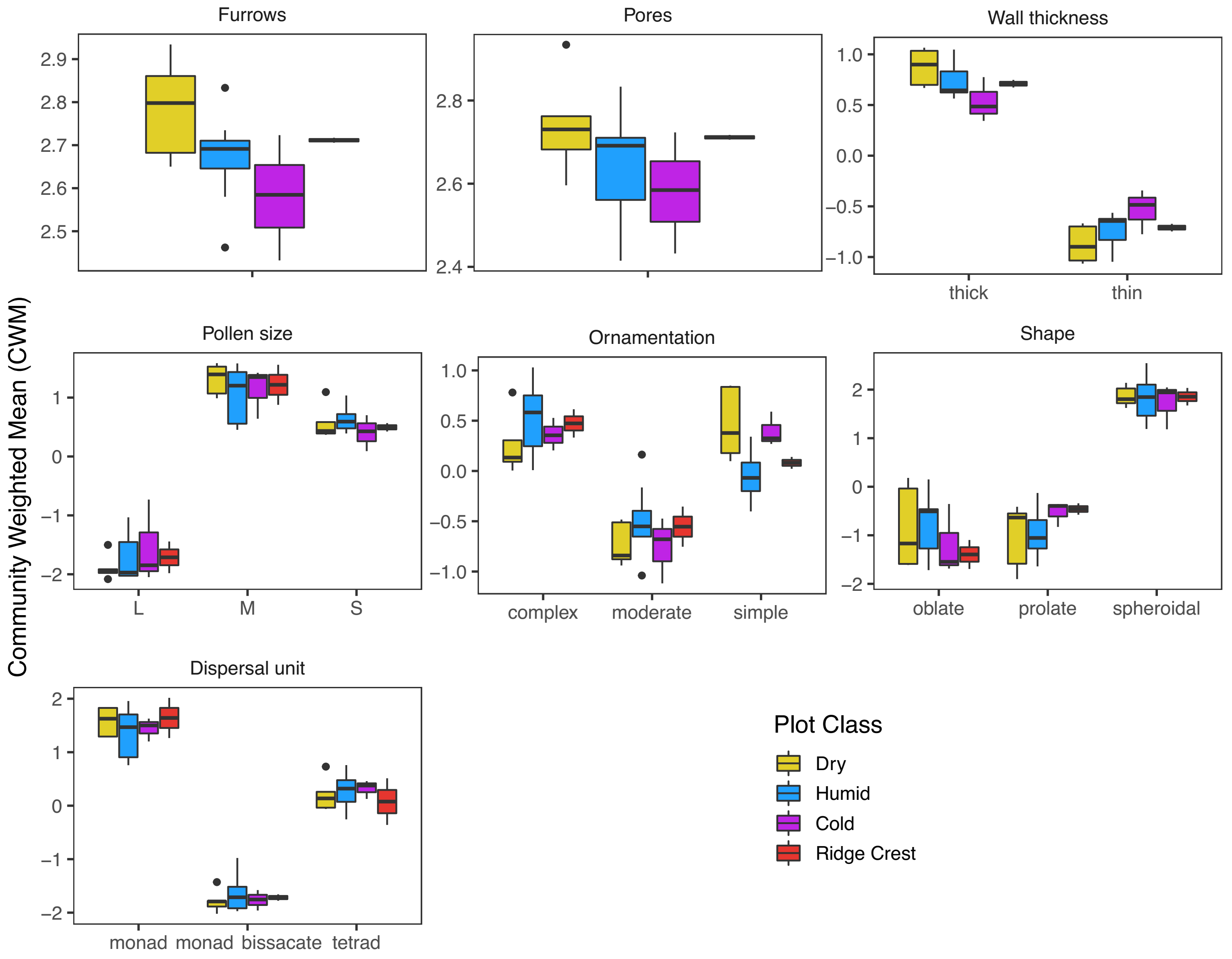

FIGURE 2 Box plots representing the community-weighted mean (CWM) pollen trait value for each laurel forest type (dry, humid, cold, ridge crest). The four box plot components are midline, median, maximum and minimum values. For the continuous traits (furrows and pores), this is calculated as the mean trait value for all taxa in the community. For categorical traits (dispersal unit, pollen size, ornamentation and wall thickness), this is calculated as the abundance of each individual class.

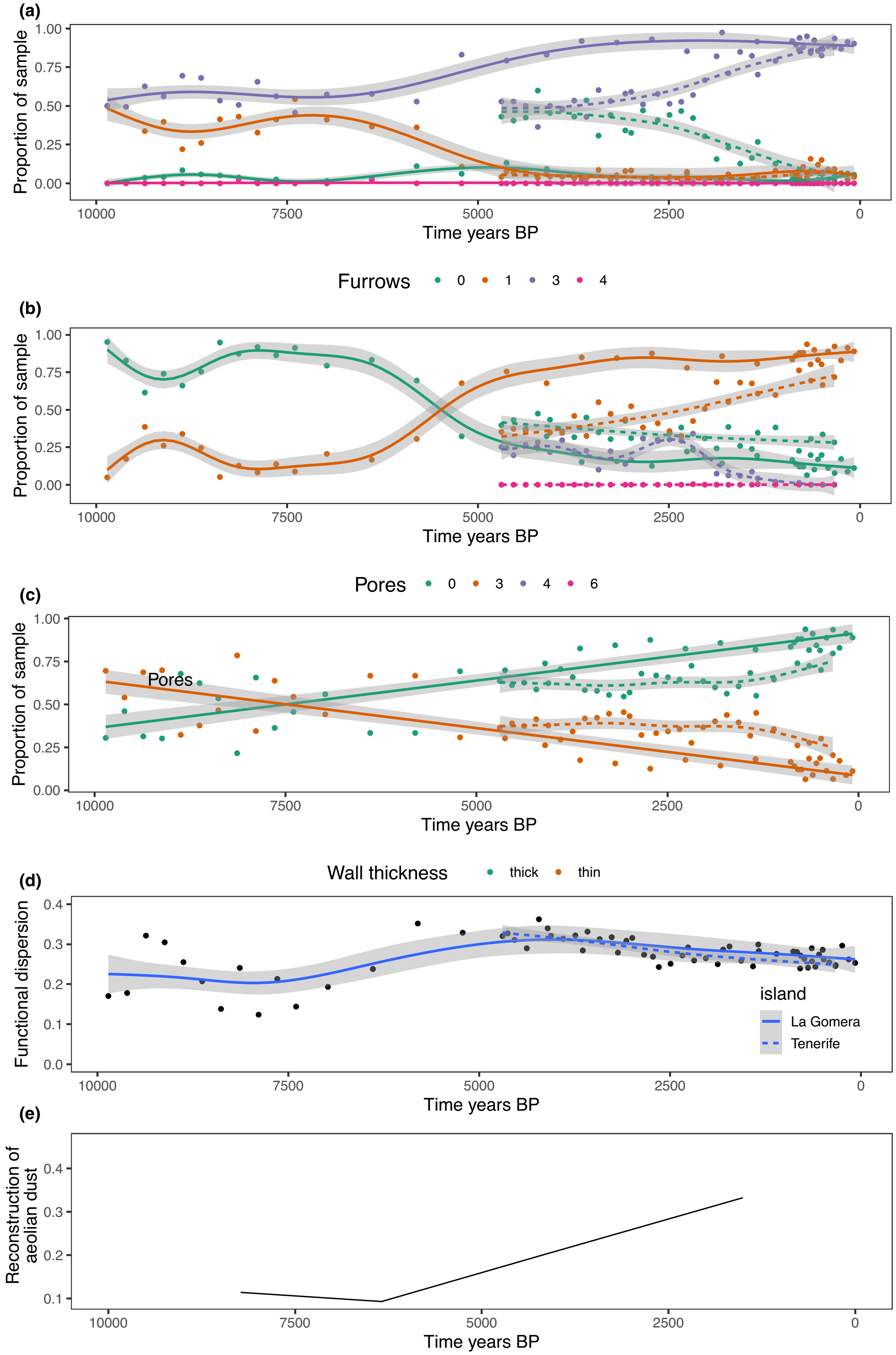

FIGURE 3 Long-term pollen profile for (a) number of furrows, (b) number of pores and (c) wall thickness for the palaeoecological record from Laguna Grande (La Gomera, 9600 cal. years BP) and La Laguna (Tenerife, 4700 cal. years BP). (d) Functional dispersion for each time point from the palaeoecological pollen data from Nogué et al. (2013) and de Nascimento et al. (2015). Note that the shorter time-series represent the pollen profile for La Laguna. (e) Reconstruction of the aeolian dust that provides a record of past changes in atmospheric circulation and aridity for the marine core GC27 (McGee et al., 2013a, 2013b). See the Supplementary information for details on palaeoclimatic data (Appendix S3).

4 | DISCUSSION

Our results are pointing towards a potential filtering process, where plants producing pollen grains with advantageous traits (e.g., high-desiccation tolerance traits in drier environments) were more represented in the community during the drier periods (Pacini et al., 2006; Franchi et al., 2011) (Figure 3). We would like to note that this paper does not aim to track evolutionary adaptations to the island environment nor to analyse whether or not pollen properties are conservative traits of selective value.

4.1 | Pollen desiccation tolerance traits: Apertures, wall thickness and pollen size

By analysing a selected set of pollen traits related to desiccation tolerance in an environmental gradient from humid to dry we were able to investigate whether laurel forest communities growing in different environments displayed distinct pollen trait assemblages. We found that laurel forest communities growing in a dry environment (450–800 m a.s.l.) produced pollen grains with apertures (furrows and pores), which are indicators of high desiccation tolerance (Figure 2). These pollen traits are thought to confer resistance to dry environments due to harmomegathic efficiency, which is the mechanism that allows variation of the pollen volume with changing moisture conditions (Franchi et al., 2011). Pollen grains with low desiccation tolerance were more prevalent at the laurel forest sites distributed within the cloud belt (e.g., humid, cold and ridge crest), where laurel forest taxa are not subject to a high risk of desiccation (del Arco Aguilar et al., 2010) (Figure 2). These taxa are, for example, species from the family Lauraceae, such as *Apollonias barbujana*, *Laurus novocanariensis*, *Ocotea foetens* and *Persea indica*.

The function of the wall is considered to be mainly protection against adverse environmental conditions such as desiccation and UV radiation (Pacini & Hesse, 2012). We found that in general, dry laurel forest showed pollen grains with thicker walls and cold laurel forest sites displayed pollen grains with thinner walls (Figure 2). It has previously been discussed that a possible advantage of thin pollen walls to plants in humid environments is that it allows rapid germination (Pacini & Hesse, 2012). In addition, it has also been suggested that to minimise the rate of water loss due to desiccation, plants produce larger pollen grains (Muller, 1979; Stroo, 2000; Ejsmond et al., 2011). In our study sites, while larger pollen grains are more prevalent on the most humid sites of the laurel forest, our results are not conclusive as medium and small-sized pollen grains were the most abundant in all forest types. Therefore, we need to treat these preliminary data with caution since our results were not conclusive.

4.2 | Pollen dispersal traits: Ornamentation, shape and dispersal unit

Another interesting result of our pollen trait analysis, specifically the presence or absence of pollen ornamentation, is related to laurel forest dispersal strategies. It has been described that pollen wall sculpturing may play a role in the attachment to insect pollinators and also to the stigma of the flower (Eriksson & Bremer, 1992; Vaknin et al., 2000; Hesse 2000; Pacini & Franchi, 2020). Over 60% of the plant taxa included in this study are classified as insect-pollinated (Olesen et al., 2007) (Appendix S6). This level of entomophily is similar to that in tropical forests where around 80% of taxa are animal-pollinated (Bush & Rivera, 1998; Weng et al., 2004; Fernández-Palacios et al., 2017). With this level of insect pollination, we would expect a dominance of pollen grains displaying complex wall ornamentation. However, the CWM analysis is not conclusive as both pollen grains with simple and complex ornamentations are equally represented across the study sites. However, we found some generalisations when focusing on the different laurel forest types. Pollen grains with simple ornamentations appear to be more prevalent in the dry laurel forest. In comparison, the CWM analysis showed that the humid laurel forest displayed the highest prevalence of pollen grains with complex and moderate ornamentations, most often associated with insect pollination (Hu et al., 2008). Our results also suggest that ornamented pollen grains are more prevalent in the core of the laurel forest that overlaps with the humid and cold laurel forest plots (Figures 1 and 2).

Finally, the analysis of dispersal units shows that the majority of plant taxa disperse as monads followed by tetrads. Similarly, the CWM analysis for pollen shape showed that the majority of pollen grains are spheroidal and do not follow any site-specific trend. The lack of conclusive results suggests that the systems we have analysed lack a sufficient range in characteristics to reveal such relationships.

4.3 | Temporal variation of pollen traits related to desiccation tolerance

Data on past environmental change from available palaeoecological records (pollen and charcoal) and palaeoclimatic data (leaf wax isotopes and aeolian dust) suggest that the laurel forests of La Gomera and Tenerife have been subject to past climate-induced and anthropogenic shifts (de Nascimento et al., 2009; Nogué et al., 2013; McGee et al., 2013a, 2013b; Tierney et al., 2017; Nogué et al., 2021; Castilla-Beltrán et al., 2021) (Appendix S3). The next question is whether the regional shift towards dryer conditions (the end of the African Humid Period) was reflected in the fossil pollen trait composition.

First, when linking pollen traits with the temporal fossil pollen data sets for La Gomera (past 9600 cal. year BP), we found that plant species producing pollen grains with thick walls and a high number of apertures (pores and furrows) increased toward the present (Figure 3a–c). This shift may respond to the greater representation of the *Morella*–*Erica* woody heath. *Morella* and *Erica* pollen grains have both three pores and furrows and thick walls, traits related to high tolerance to desiccation (Appendix S6). In addition, *Morella faya* and *Erica arborea* are considered to be pioneer species and shade-intolerant. These plant taxa also produce abundant small seeds that remain viable in seed banks for a long time as they cannot germinate under the shade of closed forest canopies (Fernández-Palacios & Arévalo, 1998). For Tenerife, the palaeoecological record is shorter (past 4700 years) and not covering the shift towards drier conditions. However, the main trend on the pollen trait profiles aligns with the previous results of more presence of plant taxa producing pollen grains with apertures and thick pollen walls.

Second, one of the most interesting conclusions is that current laurel forest taxa produce a high proportion of desiccation-tolerant pollen traits, a pollen-trait community that established around 5000 years ago and is potentially linked to a regional shift towards drier conditions. While high-desiccation tolerance pollen grains have a longer survival rate under low relative humidity enabling them to disperse further and to cross between different partners, low-desiccation pollen grains are known to survive for fewer hours after anther opening and to germinate immediately if moisture is available. If moisture is not available the survival rate is low (Franchi et al., 2011). However, results also showed that plants producing pollen grains with low desiccation tolerance prevailed during the periods of drought. This may indicate that the environmental change would not have been strong enough to filter out such traits.

Finally, the remaining question is whether pollen trait functional space changed over time or stayed constant. On the island of La Gomera fossil pollen functional trait space was small prior to 5000 cal. year BP and increased in functional dispersion from 7500 to 5000 cal. year BP (Figure 3d). Ecological theories such as niche packing (Pellissier et al., 2018) and environmental filtering (Kerkhoff et al., 2014) have suggested that the range of functional trait space in stressful environments is reduced. On the other hand, an increase in functional trait space, as shown in our analysis, might be related to a shift in the balance of species in the forest. Accordingly, our results indicate that laurel forest communities have currently a wider range of pollen traits (e.g., both high and low tolerance for desiccation) than in the past, and thus a greater diversity of trait responses (Winfree & Kremen, 2008; Pellissier et al., 2010; Matteodo et al., 2013; Kerkhoff et al., 2014; Pellissier et al., 2018). Future research should assess the relationships between pollen functional traits and other plant traits in laurel forest taxa, aiming to understand the entirety of the plant functional space and its role in forest adaptation to shifting climatic regimes.

4.4 | Limitations

The analysis of pollen traits holds great promise for improving our understanding of community and ecosystem responses to environmental change (Carvalho et al., 2019; van der Sande et al., 2019). However, there are several limitations. First, the larger amount of pollen grains released by anemophilous (i.e., high grain production) plant types when compared to entomophilous (i.e. low production) plant types (Ackerman, 2000; de Nascimento et al., 2015) may influence our findings. Lauraceae trees, which are animal-pollinated, are well known to produce a limited pollen signal (Connor et al., 2012; de Nascimento et al., 2015). For example, the 'Los Noruegos' (NOR) plot, located in the humid laurel forest type, featured the highest percentage of Lauraceae pollen grains, amounting to just 1% of the total pollen taxa analysed (Appendix S1). By comparison, in 'La Meseta' (SEC) site located in dry laurel forest, the abundance of Lauraceae pollen grains was just 0.1%. Second, the presence of *Pinus* pollen grains, despite an absence of this taxon at the study sites, requires an explanation. *Pinus* pollen is known to disperse over large spatial scales and displays several morphological traits related to wind dispersal, such as the presence of air-filled sacs (Williams, 2010) (Figure 1). *Pinus canariensis*, the sole native pine species in the Canaries, is abundant, especially in the upper regions of Tenerife, growing in a broad belt above the laurel forest. We therefore explain the presence of *Pinus* pollen grains as being dispersed from nearby trees. Third, it is likely that the robustness of the methodological framework presented here will improve with an increase in availability of pollen trait data from a wider range of plant taxa and field studies, for example, the standardization and integration of pollen traits and their interactions such as the presence or absence of pollen kit, chemical elements and phylogenetic studies.

5 | CONCLUSIONS AND NEXT STEPS

Our results indicate that pollen traits contain relevant information on plant responses to environmental change, plant survival in different environments and plant fitness over time. We suggest the following next steps:

1. To integrate pollen traits with other plant traits (e.g., leaves, roots and seeds): we suggest to integrate further pollen trait data sets from different ecosystems worldwide with plant trait data. This integration may be needed before drawing firm global conclusions concerning the drivers of the spatiotemporal distribution of pollen traits, and to enable analysis of key ongoing questions in vegetation dispersal, persistence and resilience (Franchi et al., 2011; Carvalho et al., 2019).
2. To improve the quantity and quality of the pollen trait data: new developments in computer vision and pattern recognition applied to palynology have huge potential for the analysis of pollen traits. Among the advantages of including artificial intelligence-based pollen trait classification, the most important is the improvement in accuracy and robustness of the data set. This type of analysis could be carried out on microscopic images of fossil pollen slides allowing direct measurements of pollen traits for each time-step (Viertel & König, 2022).

AUTHOR CONTRIBUTIONS

Sandra Nogué and Kathy Willis developed the study concept and original draft. Sandra Nogué, Lea de Nascimento, Laura Graham, Luke A. Brown, and José María Fernández-Palacios provided data and worked on the analyses. All authors contributed with suggestions, discussed the results and provided feedback. All authors made substantial contributions to the final article.

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DATA AVAILABILITY STATEMENT

All modern pollen data are provided in Appendix S1–S6. Fossil pollen data from Tenerife and La Gomera are available at https://github.com/ManuelSteinbauer/biodiversity-changes-on-islands

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Percentage diagram of selected modern pollen taxa

Appendix S2. Profile of pollen size, dispersal unit traits, ornamentation and pollen shape over time

Appendix S3. Location and quantitative reconstruction of published palaeoclimatic data (McGee et al., 2013a, 2013b; Tierney et al., 2017)

Appendix S4. List of study sites from La Gomera and Tenerife

Appendix S5. Description of taxa included in the analysis (modern and Holocene)

Appendix S6. Taxonomy and pollen trait characteristics of key laurel forest pollen taxa

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