Geodiversity and biodiversity on a volcanic island: The role of scattered phonolites for plant diversity and ~~reproductive fitness~~performance

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Abstract. Oceanic islands are cradles of endemism, contributing substantially to global biodiversity. A similarity in magmatic origin translates into high global comparability of substrates of volcanic islands on the oceanic crust with, however, slightly chemically or physically differentiated petrography in some places. ~~In some places, the petrography of magmatic rocks is differentiated chemically or physically.~~ Phonolites are examples of rare localities with intermediate chemical ~~traits~~characteristics between felsic and mafic and with diverse textures. They contribute to habitat heterogeneity and offer specific growth conditions in a significantly different matrix of basaltic substrates. The explicit contribution of geodiversity to island biodiversity has been little studied, despite ~~accumulating~~growing evidence of its importance on continents. On the island of La Palma, Canary Islands, isolated phonolitic rocks are conspicuous by their light colour and specific shape. Although these outcrops only cover small areas, their unique form and composition increase within-island geodiversity. To investigate how this affects biodiversity on La Palma, we sampled all vascular plant species in 120 plots on four sets of paired sites, ~~comparing~~to test if plant diversity and performance is enhanced on phonolitic ~~compared to~~with basaltic rocks~~, to test whether phonolitic rocks increase overall plant species richness and promote the reproductive fitness of plants~~. We recorded species number and abundance, individual plant height~~,~~ and diameter as proxies for aboveground resource allocation and tested for differences in vegetation cover and species composition between the bedrock types. We found higher species richness and abundance on phonolites than neighbouring basaltic substrates, and individuals of the same species were larger (in height and diameter) on phonolites compared to neighbouring basalt. An endemic woody species with two distinct varieties even appears almost

35 exclusively on the small surfaces of phonolitic rock. Despite extremely limited spatial extent, phonolitic rocks can play an important role for plant biodiversity on islands.

1 Introduction

Biodiversity is known to depend mainly on abiotic drivers, such as climate and topography (Field et al., 2009). However, the importance and explicit impacts of geodiversity on biodiversity have long been ~~under-researched~~ insufficiently researched and
40 partly ignored.~~;~~ Only recently, the~~y topic~~have started to receive more attention (~~e.g.,~~ Gray, 2004; Lawler et al., 2015; Bailey et al., 2017; Alahuhta, 2020; Barajas-Barbosa et al., 2020). Geodiversity is in many respects an abiotic equivalent to biodiversity (Gray, 2011) and represents the variability of ~~geological elements (i.e., composition)~~chemical components, surface structure, edaphic and hydrological features (Gray, 2004; Bailey et al., 2017). This variability contributes to habitat diversity and thus affects biodiversity patterns via the ~~availability~~ provisioning of ecological niches (Liu et al., 2013; Gillespie &
45 Roderick, 2014; Bailey et al., 2017). Geological elements provide unique or distinctive habitats for plants and insects, deliver initial growth conditions for vegetation or fungi formation, and are part of nutrient cycling and soil-~~g~~atmosphere interactions (Tukiainen et al., 2016).

Biodiversity is distributed unevenly throughout the world (Gaston, 2000), ~~and~~ to which oceanic islands ~~provide~~ contribute
50 disproportionately much ~~of it~~due to their high endemic richness (Kier et al., 2009). Substrates that differ in geochemistry and petrography are likely to be relevant for biodiversity on oceanic islands, where most rocks commonly share similar volcanic genesis, resulting in only slight differences in the parent material. Distinct substrates with limited extent, such as individual rock types, may function as a second isolating abiotic filter for populations in addition to the spatial isolation of oceanic islands that are known to be of outstanding importance for speciation at the global scale (Kier et al. 2009). Specific rock habitats,
55 particularly rocks that exhibit petrographic and geochemical substrates such as e.g. serpentinites, are known to be rich in habitat-specific endemics (e.g., Harrison et al., 2006; Kazakou et al., 2010). Th~~o~~ese species evolved specific adaptations to the unique nutrient contents and soil conditions and the presence of heavy metals that cannot be tolerated by other plant species (Harrison & Rajakaruna, 2011). This phenomenon is ~~also~~ known as well ~~from~~ on continen~~tal area~~s, where substrates such as serpentinite and gypsum outcrops host specialised floras and contribute to broad-scale diversity (see, e.g., Chiarucci et al.,
60 1998; Pausas et al. 2003). It~~This~~ underlines the relevance of understanding the importance of geodiversity for insular biodiversity, which is particularly vulnerable to extinction due to ~~(Paulay, 1994)~~ ~~Highly~~highly restricted ranges and small population sizes of insular endemic species (Paulay, 1994). ~~make island biotas particularly vulnerable to extinction (Paulay, 1994) and underline the relevance of understanding the importance of geodiversity for insular biodiversity.~~

65 Phonolites are rocks that occur at volcanic intraplate settings in insular and continental contexts worldwide (Garcia et al., 1986; Ackerman et al., 2015; Hagos et al., 2017). They exist in a variety of ~~forms~~geologic out~~r~~crops formed ~~in the context~~ of by

volcanic activity. Such outcrops mainly exist on continents, where they are often linked to faults and tectonic activity. Major components of these extrusive igneous rocks (formed from lava with low silica content) are alkaline feldspars together with foid minerals, nepheline, and pyroxene (Ackerman et al., 2015; Abratis et al., 2015) or their conversion products. ~~Distinctive~~

70   ~~to phonolites is their fine- to medium grain size.~~

On the island of La Palma (Canary Islands, Spain), several phonolitic rock outcrops are embedded into a ~~basaltic~~ matrix of basaltic origin (Middlemost, 1972). The dominant rock type found on La Palma is olivine and augite-titanaugite porphyric basalt, resulting from rapidly rising magma from the upper mantle (Middlemost, 1970). In contrast, there were times when a

75   sizeable magmatic chamber below the island enabled differentiation of magma and the~~,~~ removal of silica~~, and~~ thus yield~~ed~~ing ultramafic, trachytic, and phonolitic rocks (Middlemost, 1970). Phonolite trachytes (showing the exhalation of gases during eruptions) occur on various volcanic islands such as La Palma and St. Helena. On La Palma their distribution is focused on the southern (young) part of the island. The major chemistry of phonolites on La Palma is comparable to that of "average phonolites", as described by Nockolds (1954). The current volcanic activity and lava flow deriving from the Cumbre Vieja

80   volcano (Pankhurst et al.,~~ESA~~ 2021) ~~are~~ a demonstration of how phonolitic rocks became isolated by younger lava solidifying around the peaks of phonolitic rock. This event illustrates that the isolation of the investigated ~~Roque Teneguía~~phonolitic habitat~~s~~ (e.g., Roque Teneguía) is far from being a singularity but rather a process that is highly likely to have happened repeatedly on oceanic islands in general.

85   Volcanic activity with the production of tephra and lava flows is a noticeably young phenomenon in the southern part of La Palma, with eruptions as recent as now (Pankhurst et al. 2021)~~1971~~. ~~All recorded eruptions in this part took place in historic times.~~ Thus, the remnant phonolitic rocks are the tips of a former land surface that are today embedded in a basaltic matrix of noticeably immature age (Garantje et al., 1998). In consequence, weathering processes on phonolites were active on longer time scales compared to other~~the~~ surrounding rocks. In addition to petrography, differences in weathering between the rock

90   types and resulting nutrient availability also refer to different time scales of exposure. A h~~H~~igher nutrient availability enables higher plant abundances and larger plant size. Porder et al. (2004) found comparable conditions at a catena of different rock ages in the Hawaiian Islands.

Compared to basaltic lava outcrops, phonolites differ in their chemical composition and~~.~~ additionally, in colour, texture,

95   density, weathering, and formation fracturing (von Fragstein et al., 1988). ~~We observed t~~Tafoni-weathering (Formoso et al., 1989) can be observed on ~~some~~ phonolitic surfaces, indicating temperature and moisture gradients between the surface and the solid body of rocks (Brandmeier et al., 2011) ~~combined~~that appear in combination with wind exposure. Circulating leachate reaches the rock's surface and evaporates, exposing its dissolved mineral content and enabling the development of secondary mineral assemblages (Spürgin et al., 2019). These ~~that~~ can contribute to plant nutrient supply, ~~which is also why~~~~(Faccini et~~

100 ~~al., 2015, showed the effectiveness of~~ ground phonolite rock powder can be used as an effective fertilizer (Faccini et al., 2015).

For phonolites, increased release of nutrients can be mediated by bioweathering actions and plants receiving this fertilizer showed higher productivity and increased accumulation of the macronutrient potassium and of non-essential silicate in plants could be detected when applying phonolite rock powder (Tavares et al., 2018; Nogueira et al., 2021). Phonolites and the related larger-grained nepheline syenites contain significantly larger amounts of the essential nutrient potassium (see A16 for a

105 literature overview). Even if quantitatively small, such processes are of particular importance at nutrient-poor sites. In contrast, the young basalts in the southern part of La Palma are barely weathered (Carracedo et al., 19992001), appearing rough and friable with sharp spikes. We expect these petrographic and geochemical differences of parent material to affect vegetation cover and species occurrences.

110 Geologic outcrops, such as phonolites, increase microenvironmental heterogeneity, enhancing species richness at a landscape scale (Hjort et al., 2015). Increased speciation rates on isolated outcrops of scarce rocks are thought to lead to a higher percentage of endemic species than the surrounding matrix (Ricketts, 2001). Geodiversity may thus promote both species richness and endemism. However, relatively little is known about the extent to which phonolites promote species diversity in general and particularly endemism. To approach this topic theoretically,

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Pphonolitic outcrops act could be considered as small habitat islands within a basaltic matrix (Fig. 1b). The established 'species-area relationship' (SAR) and the 'species-isolation relationship' (SIR) (MacArthur & Wilson, 1967; Rosenzweig, 1995; Giladi et al., 2014) predict a smaller number of species on these small and isolated phonolitic rocks in comparison with basaltic rock outcrops in their surroundings. (From the beginning (MacArthur & Wilson, 1967), such concepts were not only
120 meant for real islands but instead took 'islands' as examples for isolated habitats (or habitat islands) within a terrestrial landscape matrix.) However, the expected higher availability of nutrients would give such habitats more favourable conditions for plant growth. Besides, it is by no means certain that the phonolitic rocks were permanently separated from each other in southern La Palma's geological evolution. Possibly, a historically much larger phonolitic rock is today largely buried by basaltic eruptions (Garantje et al., 1998). Thus, a few phonolite outcrops may serve as refugia for remnant populations
125 (Eriksson, 1996) of species specialised to phonolitic rocks.

We aim to address this knowledge gap by investigateing plant species richness and abundance on phonolites compared to surrounding basaltic lavas. To this end, we investigated the occurrences and traits of plant species in a comparative study matching basaltic and phonolitic rock formations on the island of La Palma.

130 La Palma hosts 1549 vascular plant species that are endemic to the archipelago and 479 single island endemics (hereafter SIEs) (Beierkuhnlein et al. 2021). The hyper-endemic plant species *Cheirolophus junonianus*, (Svent.) Holub, comprising its var. *junonianus* and var. *isoplexiphyllus*, (Svent.) G.Kunkel (Vitales et al., 2014a; 2014b, Beierkuhnlein et al. 2021), occurs within a range of only 3500 m² solely on La Palma (Bañares et al., 2004). Within this small range, individuals of this species occur

135   only on a few outcrops, which are almost exclusively phonolitic rocks with a chemical composition different from most of the surrounding substrates. Therefore, the species is very restricted in its range size to just a few small locations (Muer et al., 2016; Atlantis, 2021) and appears to be restricted to phonolites (Fig. 1a). This example species evokes the question if phonolites are of special importance for endemic species in the Canary Islands.

Figure 1: The endemic *Cheirolophus junonianus* (a, bottom-left) and further plant species on a phonolite rock (© Severin Irl). Aerial image of rocks of phonolites isolated in a basaltic matrix in southern La Palma (b, © Google Earth 2020).

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Phonolitic outcrops act as small habitat islands within a basaltic matrix (Fig. 1b). The established 'species-area relationship' (SAR) and the 'species-isolation relationship' (SIR) (MacArthur & Wilson, 1967; Rosenzweig, 1995; Giladi et al., 2014) predict a smaller number of species on these small and isolated phonolitic rocks in comparison with basaltic rock outcrops in their surroundings. (From the beginning (MacArthur & Wilson, 1967), such concepts were not only meant for real islands but
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160   phonolitic rocks.

We investigated the occurrences and traits of plant species in a comparative study matching basaltic and phonolitic rock formations on La Palma of comparable size, shape and extent to test the following hypotheses:

165 i. Species diversity: We expect plant species richness on phonolitic rocks to be higher than on basaltic rocks because phonolites offer more favourable plant growth conditions.

ii. ~~Species reproductive fitness~~Plant performance: Plant species populations on phonolites show a larger abundance of individuals that are taller and have greater canopy diameter than neighbouring basalts due to their advantages in

170 resource availability and porosity. We used plant performance ~~Plant height and canopy diameter were used as proxies for aboveground resource allocation and ultimately~~ as a surrogate for plant fitness.

iii. Island endemism: We expect phonolitic rocks to host more endemic plant species than basaltic rocks because of their high degree of spatial isolation, in combination with the older age of the phonolitic bedrock than the basaltic

175 matrix.

2 Methods

2.1 Study site and data sampling

We sampled four phonolitic and four adjacent basaltic rocks in the southern part of La Palma in spring 2018 (Walentowitz et al., ~~submitted~~2021; Fig. 2). Locations were identified in the field based on Middlemost (1972). The sampled phonolitic rocks

180 represented most of the overall extent of this habitat on the island, covering a large gradient of microclimate, aspect (northerness and easterness), and inclination. ~~Unfortunately, l~~Local climate data are not available for ~~the~~ individual plots, nor for the sites. Interpolated ~~model~~modelled climate data (Karger et al., 2017) show only small variations in temperature and precipitation values for our study sites (Appendix A2~~7~~). We chose comparable neighbouring pairs of phonolite and basalt consisting of one cohesive rock formation each. Outcrop pairs were chosen to match the size and microclimatic conditions

185 (aspect, slope). For each selected phonolitic and basaltic rock, we recorded plant species composition and abiotic parameters within 15 plots of 2 m x 2 m that were randomly selected within the range of accessibility on ~~the~~ phonolite and basalt. This resulted in a total of 120 plots sampled across the four pairs of phonolitic and basaltic rocks (60 plots on phonolite and 60 plots on basalt ~~in total~~).

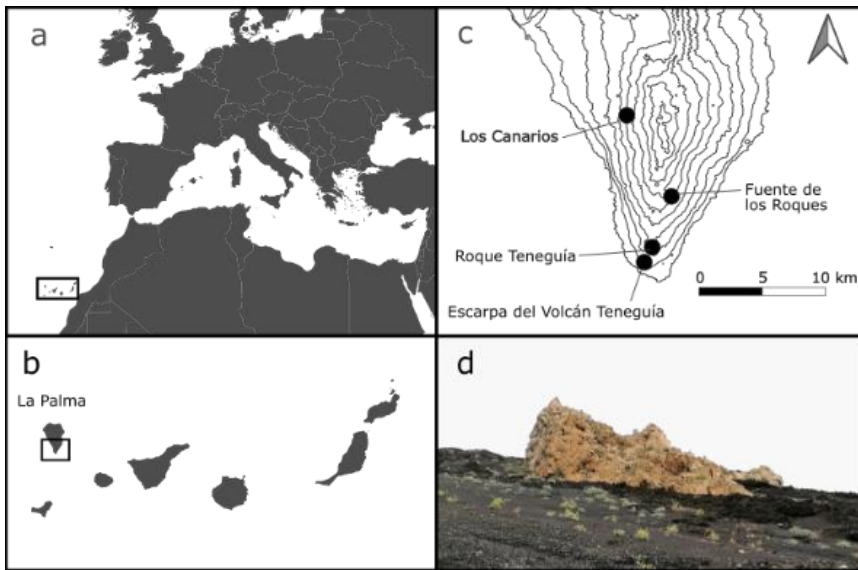



Figure 2: Location of the Canary Islands (a) and La Palma (b). Southern La Palma with our 4 study sites and contour lines at 200 m intervals (c). Phonolite rock on Southern La Palma downwards slopes of the "Roque Teneguía", located in a basaltic matrix (d, © Anna Walentowitz).

Within each plot, we recorded coordinates, aspect ~~(northerness and easterness)~~, and slope inclination. Then, we estimated rock surface rugosity using thread transects spanning the two plot diagonals: we measured the transect length along the 3D-rock surface (Walentowitz et al. 2021). Larger values of rugosity indicate higher levels of microtopography (cracks, hollows, uneven slope), while low values indicate smooth, even surfaces.

All vascular plant species within each plot, including ferns, were identified following the taxonomy of Beierkuhnlein et al. (2021) that use "Plants of the World online" (POWO, 2019) as a taxonomic backbone. The biogeographic status of each species (single-island endemic, multi-island endemic, non-endemic native and introduced) is based on Muer et al. (2016) (see extensive plant list in Appendix A~~1~~1). The number of individuals per species and plot was counted.

Plant height (length from base of the stem to the tip) and canopy diameter (widest part of the plant parallel to the ground) of all single individuals found were measured as traits.- Height, diameter, and species abundances were measured for all vascular plant species. As plant communities were dominated by perennial species, we can expect ~~to ensure~~ that vegetational differences

evolved through long-term processes and did not reflect the short-term variability of environmental conditions for this plant community dominated by perennial species. We are aware that there is a serious debate on the trade-off between different functional traits and their effect on plant fittnessgrowth responses., Hhowever, we assume that height and diameter are good proxies for different components such as survival and reproduction that contribute to plant fitness (Laughlin et al., 2020). We furthermore know that numbers of flowers and seeds might be more accurate to measure reproductive fitness when and monitoreing plants over the course of an entire reproductive cycle, but we chose plant height and width as proxies as these can be measured within a short time frameat the same time.

Lichen cover, which is abundant on the basalt, was estimated as the percent cover of each plot. Moss cover was negligible in all the plots.

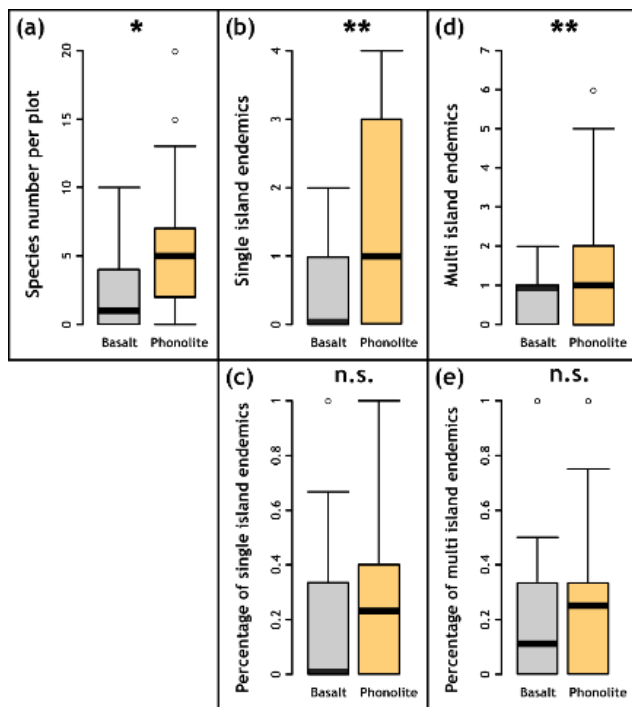
2.2 Statistical analysis

Differences in total plant species number and the number of single and multi-island endemics were analysed using Pearson's Chi-squared tests. Percentages of abundance, plant height, diameter, and SIE percentage between plots on phonolites and basalt were analysed using Mann–Whitney U tests. We conducted detrended correspondence analysis (DCA) to investigate the multidimensional aspects of vegetation composition and identify potential fundamental underlying drivers (Appendix A53). Afterwards, we applied a posthoc permutation test (10,000 repetitions) between the environmental variables (substrate, inclination, aspect and relief) and the DCA ordination axes (Appendix A64). We tested for differences in aspect, inclination, rock surface rugosity and lichen cover between phonolite and basalt using Mann–Whitney U tests.

3 Results

We recorded 68 species of vascular plants (pteridophtyes and spermatophtyes) overall. Of these species, nine were Single Island Endemics (SIE) restricted to the island of La Palma, 16 were Multi Island Endemics (MIE) co-occurring also on other islands in the archipelago, 39 were non-endemic natives, and 4 were non-natives. The SIE *Cheirolophus junonianus* was only found on phonolite, and most individuals of var. *junonianus* occurred on one isolated outcrop (Roque Teneguía) and individuals of var. *isoplexiphyllus* on another one (Escarpa del Volcán Teneguía, Fig. 2c).

We found higher plant species richness on phonolitic rocks. While 22 species were encountered on both phonolite and basalt, only eleven species were restricted to basalt, but 34 were recorded only on phonolite (Appendix A3+). Endemism groupings showed similar patterns (SIEs – phonolite: 9, basalt: 5; MIEs – phonolite: 15, basalt: 6). Besides the total number of plant species per rock type, we also found higher species richness on phonolite at the plot scale (p = 0.0164, Fig. 3 a), and higher diversity of SIEs (p = 0.00151, Fig. 3 b) and MIEs (p = 0.00727, Fig. 3 d). The percentage of SIEs (p = 0.1928, Fig. 3 c) and

MIEs (p = 0.05346, Fig 3 e) relative to total species number did not differ significantly at this scale between phonolitic and basaltic rocks.

240 **Figure 3: Perennial species per 2 x 2 m plot for basaltic (n = 60) and phonolite substrates (n = 60). a) The number of species per phonolite plot is significantly larger than foron basaltic plots. b) Phonolites have significantly more single island endemics (SIE) and (d) multi-island endemics. However, the numbers of endemic species relative to the total number of species do not differ significantly between substrates (c, e). All analyses were conducted with Pearson's Chi-squared test (a, b, c) and the Mann–Whitney U test (c, e).**

245 On phonolitic rocks, we did not find higher total plant abundance (p = 0.169, Fig. 4 a). Moreover, there was no significant difference in abundance when only considering the 23 species found in plots on both substrates (p = 0.179, Fig. 4 b).

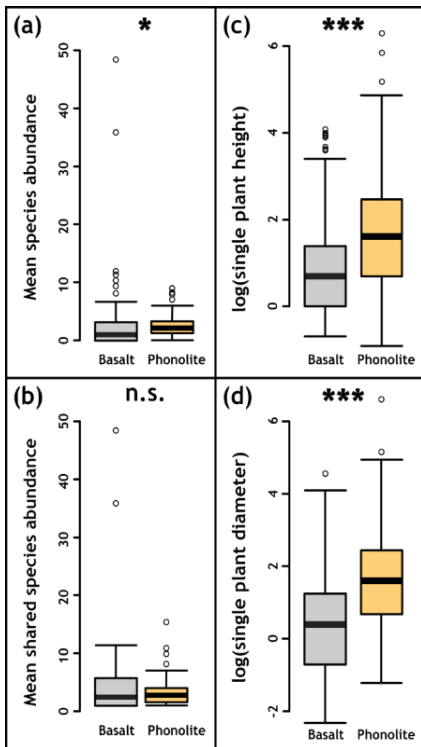



Figure 4: a) Mean abundance differs significantly between basaltic (n = 60) and phonolite substrates (n = 60), but b) considering only shared species on both substrates resulted in no significant difference between basalt (n = 39) and phonolite (n = 51). c, d) Plant height and diameter (both log10-transformed) are significantly larger on phonolite plots (n = 1560) than on basaltic plots (n = 1173). Plot size: 2 x 2 m. All analyses were conducted with the Mann–Whitney U test.

For plant species recorded on both rock types, individuals were on average taller and had wider canopies (Fig. 4c-d) on phonolitic than on basaltic rocks (Fig. 4c-d).

Plant cover only (excluding lichens) was also significantly higher (p < 0.0001, Appendix A42a) on phonolites than on basalt. Lichen cover did not show a significant difference (p = 0548, Appendix A42b).

The ordination did not show any difference in the species composition, indicating no aspects of beta-diversity at all (Appendix A5̶3̶ & A6̶4). Topographic characteristics of basalt and phonolite plots showed no differences in surface rugosity, aspect (northerness, easterness), or differences in slope inclination (Appendix A7̶5̶4).

4 Discussion

~~Phonolites host distinct vegetation compared to equivalent areas of neighbouring basaltic rocks.~~ The vegetation on phonolitic rocks differs compared to equivalent neighbouring basaltic rocks by~~is characterized~~ by exhibiting higher species richness and higher reproductive fitness of plant individuals and higher total plant cover. Higher numbers of single- and multi-island endemics on phonolites also reflect augmented total species numbers on this rock type.

Phonolite rocks on La Palma and other oceanic islands are arranged as habitat islands in a basaltic matrix (Fig. 1b). On La Palma, the total area of phonolite outcrops̶ is tiny compared ~~with~~ to the area of the basaltic matrix. Thus, encountering more species on phonolites than on basalt aligns with our hypotheses but defin̶es the area effect on species richness, which predicts species number to be lower in the phonolite habitat. Differences in species numbers might be accounted to lower-than-expected species growing on basalt or on higher-than-expected species numbers on phonolites. ~~This makes the greater number on phonolite even more remarkable. However, o~~Our findings are congruent with studies,̶ which did not find a species-area relationship or relationships with a less steep slope on habitat islands (Matthews et al., 2016; Deák et al., 2018). Reasons might be unrealised niches due to unsaturated evolutionary dynamics in this young and isolated system. Environmental filters (Liu et al., 2020) enhancing growth conditions on phonolite outcrops may also exist, consistent with our findings that ~~the~~ plants are larger on phonolites. Characteristics of rocks include, amongst others, texture, appearance, colour (potentially translating into differing rock surface temperature), fracture, streak and̶, hardness ~~and more.Several~~ ~~Following~~Consequently, mutually non-exclusive drivers may explain th̶e observed̶is̶ phenomenon: 1) chemistry 2) age and 3) phonolite-specific surface texture and colour (as a proxy for rock surface temperature)~~, 2) colourtemperature, 3) chemistry, and 4) age~~.

~~1) We observed deeper fractures in phonolitic rocks than in other volcanites on La Palma Island. Besides, phonolitic rocks show a much smoother surface roughness than their surrounding matrix. Basaltic rocks seem to possess a more dynamic relief, mainly attributed to their origin in congealed lava flows, typically found on oceanic islands. When testing rock surface rugosity, there were no significant differences between phonolitic and basaltic rocks. Hence, we argue that surface texture does not play a role for higher plant growth response, richness and abundance observed on phonolites.~~

~~2) Most phonolitic rocks in a basaltic matrix are visually brighter than basalt. We expected that phonolites hold a higher albedo than surrounding rocks and therefore expected them to have a reduced surface temperature compared to volcanic outcrops with darker colouring, such as basalt. However, in an experiment with differently coloured bricks Hall et al. (2005) showed that the~~

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3~~1~~) T~~Grain size and t~~he rather porphyric arrangement of phonolites imply ameliorating plant growing conditions on this rock type. The chemical composition of phonolites has been described as nutrient-rich as it has traditionally been ground up and used as an inorganic fertilizer (von Wilpert & Lukes, 1998; Ramos et al., 2006; Schoen et al., 2016). Phonolites consist of the potassium-rich nepheline, which dissolves much faster than other potassium sources (Manning, 201~~00~~9). This may explain

300 increased plant growth on phonolites. Weathering processes may act as driving forces for the establishment and germination of plants as they increase plant-available nutrients on these outcrops. Since ground phonolitic rock fertilizer is used to provide crops and trees with potassium (von Wilpert & Lukes, 1998; Schoen et al., 2016), plants growing on phonolites might profit from this rock characteristic. Basaltic rock powder has also been used as fertilizer in rare cases but according to Manning (2010) this is mainly due to geologically unclear assignments (potassium-rich trachyte is often assigned to basalt). ~~,~~ Other

305 studies state that nutrient availability on basalt can be part of a feedback cycle where weathering releases essential nutrients that are key for plants to survive but the occurrence of plants on basalt can also lead to higher availability of macronutrients (Ca, M~~agnesium~~g, K), micronutrients (Fe), and non-essentials like Si and Na (Hinsinger et al., 2001).~~but according to Manning (2009) this is mainly due to geologically unclear assignments (potassium-rich trachyte is often assigned to basalt). Furthermore, he points out that~~Although basalt and phonolite have both been reported to enhance nutrient conditions for plants, basalt was

310 ~~reporte~~reported~~is~~ to be ~~another~~ a potential but smaller source of potassium than phonolite (Manning 2010). Additionally, phonolite rocks in Southern La Palma are several hundred years older than the surrounding basalt (Carracedo et al. 1999) and have thus been exposed to weathering for longer timescales.

315 4~~2~~) The age of geological formations influences plant diversity and species composition (Whittaker et al., 2008; Hulshof & Spasojevic, 2020). As noted in previous studies (Carracedo et al., 1999~~2001~~), the Cumbre Vieja rift on La Palma has evolved throughout several eruptions and therefore contains lava formations from different ages as well as slightly different mineralogical compositions. The current volcanic activity and lava flows at the Cumbre Vieja are a live example of this geological process (Pankhurst et al. 2021). The known phonolite rocks on La Palma are located in the geologically young

320 southern part of the island. Consequently, we can assume that they are all in a stage of high ecological opportunities resulting in unsaturated niches (Whittaker et al. 2008). An interplay between erosion-driven uncovering of lava-covered phonolite rocks and new lava flows may strongly influence the vegetation on those rocks. We observed partly buried phonolites on which the survival of plants or seedlings during volcanic events was improbable (Garantje et al., 1998). Carracedo et al. (1999~~2001~~) showed that the last phonolite formation occurred in 1585, while there have been basaltic outbreaks until ~~1977~~now (Pankhurst

325 et al. 2021). Thus, age differences between phonolitic and basaltic outcrops might influence plant composition and performance. ~~A geological map provided by Carracedo et al. (2001) shows that most phonolitic rocks surrounded by lava flows are much older than 1585.~~The younger age of basaltic rocks might have the consequence that evolutionary time scales were too short, niches remain empty, and basaltic outcrops host less species compared phonolites. In any case, the age of the substrate is significantly influencing the species numbers and plant performance. In addition, species composition might also

330 be influenced by age differences of underlying rock material as 19 species including *Cheirolophus junonianus* ~~with its var. junonianus and var. isoplexiphyllus~~ can solely be encountered on phonolitic rocks (Muer et al., 2016). Interestingly, overall vegetation on phonolites cannot be considered to be distinct from basalt and these phonolite-specific species do not majorly drive vegetation patterns on this rock type. However, it is well known that habitat diversity on islands leads to higher species richness (Hortal et al., 2009). Phonolites offer an additional habitat for plants to grow on and hereby contribute to plant species

335 richness on La Palma (Irl et al., 2015).

3) Besides petro-chemical characteristics and rock age, the surface structure and colour of phonolites might be suspected to drive plant patterns on such rocks. We observed deeper fractures in phonolitic rocks than in other volcanites on La Palma. Besides, phonolitic rocks show ~~in the field~~ a much smoother surface roughness than their surrounding matrix. Basaltic rocks

340 seem to possess a more dynamic relief, mainly attributed to their origin in congealed lava flows, typically found on oceanic islands. Nevertheless, when testing rock surface rugosity, there were no significant differences between phonolitic and basaltic rocks. Hence, we argue that surface characteristics do not play a role for higher plant growth response, richness and abundance observed on phonolites. Besides fractures, another visual observation was that phonolites are of lighter colour than their surrounding basaltic matrix. We expected that phonolites hold a higher albedo than surrounding rocks and therefore expected

345 them to have a reduced surface temperature compared to volcanic outcrops with darker colouring, such as basalt. However, in an experiment with differently coloured bricks Hall et al. (2005) showed that the albedo of white surfaces only leads to significantly lower temperature of the material when the surface temperature falls below air temperature. With monthly temperatures between 17 and 25° C within large areas of oceanic islands (Harter et al., 2015), no major temperature differences between basalt and phonolite surfaces can be expected. We therefore consider that this effect has no major impact on plants'

350 habitat suitability.

While rock chemistry and age seem to increase species numbers on phonolites, these rock characteristics do not lead to higher percentages of endemic plants or a compositional distinct vegetation. ~~The differential geology itself results in a specialized flora of those habitat islands (Kruckerberg, 1991).~~ Even though the ~~hyper~~ endemic *Cheirolophus junonianus* with its two

355 varieties var. *junonianus* and var. *isoplexiphyllus* is confined to phonolites, the percentage of single island endemics on phonolites was not significantly higher, refuting our expectations~~, though the numbers of endemic species were significantly higher. Lessons learned from other outcrops (Kruckerberg, 1991) cannot be applied to phonolitic rocks on La Palma, and the functioning of phonolites as islands of speciation within a sea of basalt does not seem to apply. However, a~~As most individuals

of the typical variety of *Cheirolophus junonianus* occur on one isolated outcrop and individuals of var. *isoplexiphyllus* on another one (personal observation), it could be ~~supposed~~suspected that a very local allopatric speciation by adaptive radiation or an ongoing genetic drift could be the underlying cause (Vitales et al., 2014a; 2014b). Thus, the differential geology of phonolites itself does not result~~s~~ in a specialized flora of habitat islands, contrary to e.g., Kruckerberg (1991), and populations of *Cheirolophus junonianus* ~~have to~~must be seen in another context. ~~However, c~~Considering the geologic history of the islands South (Garantje et al., 1998) it is a more ~~One~~ possible explanation ~~for~~ that this singularity presumes that *Cheirolophus junonianus* belongs to a relict population of plants that were once widely distributed on phonolitic rock before these were cover~~sp~~ed mainly ~~by~~in a basalt~~ic matrix~~. Consequently, lessons learned from other outcrops (Kruckerberg, 1991) cannot be adapted to the phonolitic rocks on La Palma, and the functioning of phonolites as islands of speciation within a matrix of basalt does not seem to apply. However, considering *Cheirolophus junonianis* to be a remnant plant population on phonolites raises, on the one hand, the question if the species might increase community resilience and ecosystems stability, including nutrient cycling, as hypothesized by Eriksson (2000) for remnant populations in general. On the other hand, possible extinction debts might lead to the disappearance of the species in the future and only the continuous monitoring of these populations can help to answer these questions. ~~Species composition might be influenced by age differences of underlying rock material as 19 species inclusive like *Cheirolophus junonianus* and its var. *junonianus* and var. *isoplexiphyllus* can solely be encountered on phonolitic rocks (Muer et al., 2016). However, It is well known that habitat diversity on islands leads to higher species richness (Hortal et al., 2009). Phonolites offer an added habitat for plants to grow on and contribute to plant species richness and endemism on La Palma (Irl et al., 2015).~~

When looking at the role of geologic promotion of biodiversity, there are several studies addressing serpentinite rocks and serpentine soils. On those rocks and soils, ~~considerable amounts of toxic heavy metals,~~ low amounts of essential nutrients (N, K, and P), and a low calcium-to-magnesium ratio relate to high rates of endemism and a specialized flora (Chiarucci, 2003; Harrison et al., 2006). These serpentinite-tolerating species are restricted to a harsh environment by dominant competitors in a less harsh matrix. On phonolitic rocks, more favourable growing conditions resulting in higher plant richness and abundances seem to prevail. Compared to serpentinite rock studies, the surrounding matrix is built up by the potentially harsher basaltic rocks resulting in lower plant growth response.

The geological history of basaltic rocks depends on a series of different volcanic eruptions, assuming a more considerable chemical variability, whereas phonolites seem to build upon one or just a few volcanic events (Carracedo et al., 1999~~2001~~). The long chronology of volcanic eruptions on the Canary Islands and their ancestors reveals a high likeliness that most of the eruptions resulted in basaltic, only a few in phonolitic formations. Plants growing on basalt experienced larger environmental gradients since basalt is omnipresent on the islands. Contrasting, plants growing only on phonolites did not experience larger environmental gradients. ~~In accordance, we observed plants on basaltic rocks to be more generalist than plants on phonolitic rocks.~~

We are not aware of other studies conducted in locations where phonolites can be encountered that explore their potential role
395 as exceptional plant habitat islands, even though phonolites can be found all over the world (Garcia et al., 1986; Ackerman et al., 2015; Hagos et al., 2017). Therefore, further investigation is needed to ~~figure out~~ investigate whether the patterns encountered on La Palma may also be found on comparable phonolitic rocks in other areas of the world. Their benefits for biodiversity found in this study need to be recognized and valued. Especially for isolated areas such as islands, phonolites can contribute to small-scale biodiversity hotspots and our findings suggest that they should be conserved.

5 Conclusion

400
Phonolites provide unique habitat conditions for plants on oceanic islands ~~and exhibit distinct vegetation~~ compared with surrounding areas. Higher species numbers and abundances as well as higher plant ~~growth responses~~ performance underlines the importance of these rocks for the vegetation on ~~these~~ oceanic islands ~~which are globally dispersed~~ spread all over the world. Despite the small total area covered by phonolites they play a significant role in enhancing plant biodiversity on the island of
405 La Palma. Our results suggest that exceptional rock outcrops like phonolites contribute to a better understanding of the ~~distribution~~ formation of~~and~~ plant diversity ~~drivers~~ on volcanic islands ~~such as La Palma.~~ ~~through exceptional rock outcrops like phonolites~~. As oceanic islands have always been formed through volcanic activity on the oceanic crusts, the combination of basaltic and phonolitic rocks is highly likely a regular pattern in Earth history.

Appendix

410 **A1: References of selected chemical components of basaltic and phonolitic substrates. B) indicates basaltic substrats or treatments, P) phonolitic and N) nepheline syenite (phonolite equivalent with larger grain size) ones.**

Study	System/ study	Ca	Mg	K	Mn	P	Fe
Roqueto do Reis (2021; thesis)	Substrate used in experiments	B) 8.54% P) 1.76% CaO	B) 4.74% P) 0.32% MgO	B) 1.25% P) 8.05% K_2O	B) 0.21% P) 0.25% MnO	B) 0.42% P) 0.07% P_2O_5	B) 14.82% P) 3.87% Fe_2O_3
Garcia et al. (1986)	Field work (Kaula Isl.)	P) 1.74% CaO	P) 1.93% MgO	P) 4.48% K_2O	P) 0.31% MnO	P) 0.64% P_2O_5	P) 3.33% Fe_2O_3; P) 1.74% FeO
Hagos et al. (2017)	Field work (Axum)	P) 1.12% CaO	P) 0.05% MgO	P) 4.94% K_2O	P) 0.30% MnO	P) 0.04% P_2O_5	P) 5.47% Fe_2O_3

Manning (2010)	Review	B) 9.47% N) 2.31% CaO	B) 6.73% N) 0.77% MgO	B) 1.10% N) 5.58% K$_2$O	B) 0.20% N) 0.15% MnO	B) 0.35% N) 0.13% P$_2$O$_5$	B) 3.79% N) 2.25%; Fe$_2$O$_3$ B) 7.13% N) 2.05% FeO

A2: Interpolated data from Climate models for our research sites bases on the Chelsa Climate Data (Karger et al., 2017).

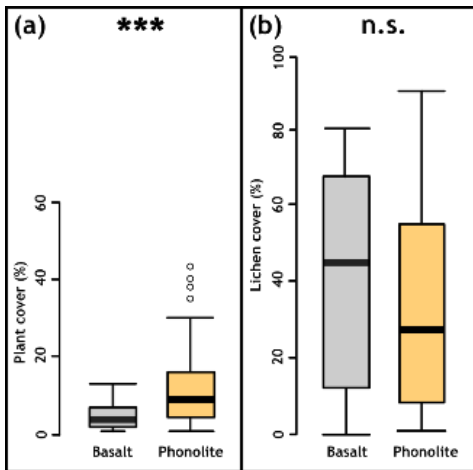
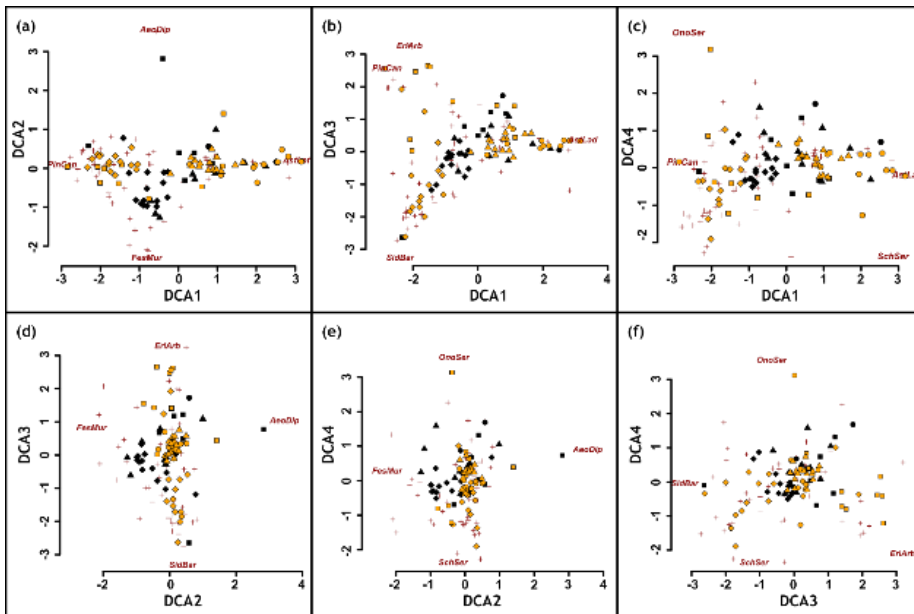
Site	Annual mean temperature [C °]	Annual precipitation [mm]
Los Canarios	16.7	651
Fuente de los Roques	18.2	536
Roque Teneguía	16.5	633
Ecarpa del Volcán Teneguía	18.8	517

415 **A31: Complete list of all study species encountered on phonolites (P) and basalt (B) including their status as single island endemic (SIE), multi-island endemic (MIE), native (nat.) and introduced (intr.). The taxonomy follows the standards of "Plants of the World online" (POWO 2019) updated and adapted to the FloCan Checklist (Beierkuhnlein et al., 2021).**

Species	Family	Rock type	Status	woody	perennial
Aeonium arboreum ssp. *holochrysum* (H.Y.Liu) Bañares	Crassulaceae	B/P	MIE	1	1
Aeonium davidbramwellii H.Y.Liu	Crassulaceae	B/P	SIE	1	1
Aeonium diplocyclum (Webb ex Bolle) T.H.M.Mes	Crassulaceae	B	MIE	1	1
Aichryson bollei Webb ex Bolle	Crassulaceae	P	SIE	0	1
Aira caryophyllea L.	Poaceae	B/P	nat.	0	0
Allium canariense (Regel) N.Friesen & P.Schönfelder	Amaryllidaceae	P	MIE	0	1
Anogramma leptophylla (L.) Link	Pteridaceae	B	nat.	0	0
Anthoxanthum odoratum L.	Poaceae	P	nat.	0	1
Arabidopsis thaliana (L.) Heynh.	Brassicaceae	B/P	nat.	0	0
Arenaria leptoclados (Rchb.) Guss.	Caryophyllaceae	B/P	nat.	0	0
Argyranthemum haouarytheum Humphries & Bramwell	Asteraceae	P	SIE	1	1
Astydamia latifolia (L.f.) Baill.	Apiaceae	P	nat.	1	1
Bituminaria bituminosa (L.) C.H.Stirt.	Fabaceae	P	nat.	1	1
Brassica oleracea L.	Brassicaceae	B	intr.	0	1
Bystropogon origanifolius var. *palmensis*	Lamiaceae	B/P	SIE	1	1
Cardamine hirsuta L.	Brassicaceae	B	nat.	0	0
Cheirolophus junonianus (Svent.) Holub	Asteraceae	P	SIE	1	1
Cosentinia vellea ssp. *bivalens* (Reichstein) Rivas Mart. & Salvo	Pteridaceae	B/P	nat.	0	1
Crassula campestris (Eckl. & Zeyh.) Endl.	Crassulaceae	B	intr.	0	0

Davallia canariensis (L.) Sm.	Davalliaceae	B/P	nat.	0	1
Echium brevirame Sprague & Hutch	Boraginaceae	B/P	SIE	1	1
Erica arborea L.	Ericaceae	P	nat.	1	1
Erigeron bonariensis L.	Asteraceae	P	nat.	0	0
Erodium botrys (Cav.) Bertol.	Geranicaeae	P	nat.	0	0
Festuca muralis Kunth	Poaceae	B	nat.	0	0
Filago germanica (L.) Huds.	Asteraceae	B	nat.	0	0
Galium aparine L.	Rubiaceae	B/P	nat.	0	0
Geranium molle L.	Geraniaceae	P	nat.	0	0
Geranium purpureum Vill.	Geranicaeae	P	nat.	0	0
Hemionitis gluckuk Christenh.	Pteridaceae	P	nat.	0	1
Hemionitis guanchica (Bolle) Christenh.	Pteridaceae	B/P	nat.	0	1
Holcus lanatus L.	Poaceae	P	nat.	0	1
Hyparrhenia hirta (L.) Stapf	Poaceae	B/P	nat.	0	1
Kleinia neriifolia Haw.	Asteraceae	P	MIE	1	1
Lavandula canariensis Mill.	Lamiaceae	P	MIE	1	1
Lobularia canariensis (DC.) L.Borgen	Brassicaceae	P	MIE	1	1
Medicago truncatula Gaertn.	Fabaceae	P	nat.	0	0
Mercurialis canariensis Obbard & S.A.Harris	Euphorbiaceae	P	MIE	0	0
Micromeria herpyllomorpha Webb & Berthel.	Lamiaceae	B/P	SIE	1	1
Monanthes muralis (Webb ex Bolle) Hook.f.	Crassulaceae	B/P	MIE	0	1
Ononis serrata Forssk.	Fabacea	P	nat.	0	0
Opuntia ficus-indica (L.) Mill.	Cactaceae	P	intr.	1	1
Parietaria debilis G.Forst.	Urticaceae	P	nat.	0	0
Paronychia canariensis (L.f.) Link	Caryophyllaceae	P	MIE	1	1
Periploca laevigata Aiton	Apocynaceae	P	nat.	1	1
Phagnalon purpurascens Sch.Bip.	Asteraceae	P	nat.	1	1
Pinus canariensis C.Sm. ex DC.	Pinaceae	P	MIE	1	1
Polycarpaea aristata (Aiton) C.Sm. ex DC.	Caryophyllaceae	B/P	MIE	0	1
Polycarpaea tenuis Webb ex Christ	Caryophyllacea	P	MIE	0/1	1
Polypodium macaronesicum A.E.Bobrov	Polypodiaceae	B/P	nat.	0	1
Pteridum aquilinium (L.) Kuhn	Pteridaceae	P	nat.	0	1
Pterocephalus porphyranthus Svent.	Caprifoliaceae	P	SIE	1	1
Rubia fruticosa Aiton	Rubiaceae	P	nat.	1	1
Rumex bucephalophorus ssp. canariensis (Steinh.) Rchb.f.	Polygonaceae	B	nat.	1	1
Rumex lunaria L.	Polygonaceae	B/P	MIE	1	1
Schizogyne sericea (L.f.) DC.	Asteraceae	B/P	nat.	1	1

Sideritis barbellata Mend.-Heuer	Lamiaceae	B/P	SIE	1	1
Solanum villosum Mill.	Solanaceae	P	nat.	0	1
Sonchus hierrensis (Pit.) Boulos	Asteraceae	P	MIE	1	1
Sonchus oleraceus L.	Asteraceae	B/P	nat.	0	0
Stachys arvensis (L.) L.	Lamiaceae	B/P	nat.	0	0
Todaroa aurea (Aiton) Parl.	Apiaceae	P	MIE	0	1
Tolpis laciniata Webb	Asteraceae	B/P	MIE	0	1
Trifolium arvense L.	Fabaceae	B	nat.	0	0
Tuberaria guttata (L.) Fourr.	Cistaceae	B	nat.	0	1
Umbilicus gaditanus Boiss.	Crassulaceae	B/P	nat.	0	1
Valeriana dentata (L.) All.	Valerianaceae	P	intr.	0	0
Wahlenbergia lobelioides (L.f.) Link ssp. *lobelioides*	Campanulaceae	B	nat.	0	0

420

A42: **Vegetation cover on basaltic and phonolite plots. (a) Plant cover showed** ~~the same result~~significant, (**p < 0.001, Mann–Whitney U test**)~~ and~~. **(b)** ~~L~~ichen cover showed no significant difference between the substrates (p > 0.05, Mann–Whitney U test).

A53: Detrended Correspondence Analyses (DCA) shows no clear difference between phonolite and basaltic rock vegetations. Yellow dots show phonolite plots, black dots basalt plots, dark red a subset of species centroids. Species names chosen based on most extreme values along the gradients.

A64: A posthoc permutation test (10,000 repetitions) between the DCA ordination axes and the environmental variables (substrate, inclination, aspect and relief) showed no significant differences between phonolite and basalt. Obviously, the variation shown in the DCA does not depend on the substrate (but there is a relationship between northerness and the fourth dimension DCA4).

	DCA1&DCA2	DCA1&DCA3	DCA1&DCA4	DCA2&DCA3	DCA2&DCA4	DCA3&DCA4
Substrate	p = 0.623	p = 0.503	p = 0.768	p = 0.289	p = 0.959	p = 0.439
Inclination	p = 0.490	p = 0.946	p = 0.315	p = 0.523	p = 0.108	p = 0.365
Northerness	p = 0.914	p = 0.526	p = 0.032	p = 0.875	p = 0.933	p = 0.921
Easterness	p = 0.293	p = 0.564	p = 0.310	p = 0.429	p = 0.213	p = 0.426
Rugosity	p = 0.212	p = 0.387	p = 0.324	p = 0.875	p = 0.933	p = 0.921

A754: Environmental plot characteristics. Inclination on phonolites was (despite efforts to sample similar environments) significantly higher than on basalt. Components of exposition (northerness and easterness) and rugosity showed no significant differences (unpaired Whitney test).

	Rugosity (m)	Northerness	Easterness	Inclination (°)
Mean Basalt	3.557	0.01407	0.04970	43.0
Mean Phonolite	3.643	-0.09062	0.04303	53.8
p-Value	0.7781	0.6525	0.8827	0.0277

Code availability

Only standard tests and plotting commands in R were used for data analysis. The code is available on request from the corresponding author.

445 **Data availability**

Any data supporting the findings of this study are available within the supplementary materials of this article and were taken from Walentowitz et al. ({2021submitted)}.

Authors contributions

C.B., S.D.H.I., D.K., L.S. and A.J.W. developed the research idea, D.K., L.S. and A.J.W. conducted the field work, analysed
450 the data and led the writing process. All authors developed the methods, discussed the results and contributed to the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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