LETTER

Long-term trajectories of non-native vegetation on islands globally

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Abstract

Human-mediated changes in island vegetation are, among others, largely caused by the introduction and establishment of non-native species. However, data on past changes in non-native plant species abundance that predate historical documentation and censuses are scarce. Islands are among the few places where we can track human arrival in natural systems allowing us to reveal changes in vegetation dynamics with the arrival of non-native species. We matched fossil pollen data with botanical status information (native, non-native), and quantified the timing, trajectories and magnitude of non-native plant vegetational change on 29 islands over the past 5000 years. We recorded a proportional increase in pollen of non-native plant taxa within the last 1000 years. Individual island trajectories are context-dependent and linked to island settlement histories. Our data show

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that non-native plant introductions have a longer and more dynamic history than is generally recognized, with critical implications for biodiversity baselines and invasion biology.

INTRODUCTION

Humans have become the overwhelming force behind changes in island biodiversity in the Anthropocene (Russell & Kueffer, 2019). Many native island biotas continue to decline in diversity and numerous species are heading towards extinction (Bellard et al., 2017; Spatz et al., 2017), in part because islands have also become hotspots of non-native species introductions (Dawson et al., 2017). A total of 26% of all islands have already accumulated more non-native than native vascular plant species (Essl et al., 2019). Further, new evidence shows that vegetation turnover rates increased 11-fold since human settlement on islands (Nogué et al., 2021), leading to the emergence of novel ecosystems characterized by altered species compositions and structural features (e.g. Devkota et al., 2020; Ewel et al., 2013).

For some islands, substantial restoration actions and conservation efforts are being advocated and undertaken to protect endemic island biodiversity, such as invasive species eradication (Jones et al., 2016; Kaiser-Bunbury et al., 2010; Tapia et al., 2022). On other islands where traditional societies have been living for millennia or centuries, the revitalization of traditional land management approaches counter to modern industrial land-use practices may be resulting in better conservation outcomes for endangered species (Fletcher et al., 2021; Russell & Kueffer, 2019). Tracing the transition from natural dynamics to a human-dominated world to obtain palaeoecologically derived baseline information is necessary if achievable ecosystem restoration and conservation goals are desired (Barak et al., 2016; Nogué et al., 2017; Willis & Birks, 2006).

Islands exhibit unique histories of human-mediated vegetation change depending on (1) the onset of initial and subsequent human colonization events, and (2) the associated type and impact of land use and non-native species introductions (throughout this article colonization refers to humans, not colonization by other species). Human arrival on an island is thus a key event determining subsequent biodiversity change (Nogué et al., 2021; Russell & Kueffer, 2019). Overall, evidence suggests that biodiversity changes due to 'natural' drivers of change (e.g. climate, volcanism) have been overwhelmed by the impacts of anthropogenic drivers after the first arrival of people (Russell & Kueffer, 2019; Wilmshurst et al., 1997). Habitat destruction, unsustainable exploitation of resources and the introduction of non-native

species (including diseases associated with novel microorganisms and pathogens) has resulted in extinction of local populations or species (Wood et al., 2017). The spread of non-native species in contemporary times and projections into the future show that biological invasions are an especially important driver of island biodiversity change (Fernández-Palacios et al., 2021; Leclerc et al., 2018; Lenzner et al., 2020; Russell & Kueffer, 2019). With the advent of European colonization worldwide (after 1492 AD), ongoing land-use change, globalized trade and subsequent increased urbanization amplified these changes (Fernández-Palacios et al., 2021; Russell & Kueffer, 2019; Steibl et al., 2021). An extreme example of modern human-driven biodiversity alteration can be found on the volcanic island of Ascension (South Atlantic Ocean), where in an attempt to green the island, artificial ecosystems consisting almost entirely of non-native species were established in the nineteenth century (Wilkinson, 2004). Largely treeless areas were transformed into novel ecosystems of tropical cloud forests dominated by non-native species (Wilkinson, 2004). This landscape transformation has led to severe reductions in native plants and extinctions, and the potential for future extinctions (Cronk, 1997).

Trends in biodiversity change on islands can be highly context dependent, resulting in differences in ecosystem transformation and biodiversity change. The large island of New Guinea was settled by people more than 50,000 years ago, but retains the world's richest island flora (Cámara-Leret et al., 2020). Fiji and Vanuatu were first colonized 3000 BP and New Zealand around 750 BP, resulting in contrasting ecosystem transformation and biodiversity change, for example, deforestation and reduced native species' population sizes or extinctions (Ash, 1992; Lebot & Sam, 2019; Wilmshurst et al., 2011). By contrast, the Galápagos Islands were settled in the nineteenth and twentieth centuries (Tye, 2006), which is comparatively late in human history, with numerous endemic species currently facing extinction (Bush et al., 2022).

Besides anthropogenic pressures, the biogeographical and environmental properties of islands are known to shape their susceptibility to invasion (Blackburn et al., 2016; Essl et al., 2019; Helmus et al., 2014; Moser et al., 2018). More isolated islands, such as the Hawaiian group (approximately 3650 km from the nearest mainland) or the Tongan Islands (approximately 3340 km) (Moser et al., 2018; Weigelt et al., 2013), are more prone

to the establishment of non-native species than less isolated island systems such as the Canaries (96 km) (Fernández-Palacios et al., 2022). The main explanations are that isolated islands exhibit lower competition among the few native species for available resources resulting in an often naïve native flora and fauna that can be poor in characteristics that make them less competitive against introduced non-natives (Allen et al., 2006; Whittaker & Fernández-Palacios, 2007). As a consequence, islands have accumulated high numbers of non-native species from a wide range of taxonomic groups, including groups previously absent from islands (Moser et al., 2018), often with severe impacts on native species (Bellard et al., 2017). While recent work has shown that the accumulation of non-native species has been prolific in recent decades on continents as well as islands (Seebens et al., 2017), it remains unknown when and how many non-native species were introduced to islands in previous centuries and millennia.

Fossil pollen time-series from chronologically dated sedimentary sequences offer the opportunity to unravel the dynamics of non-native species over millennia. Palaeoecological approaches have already been successful in reconstructing how island vegetation responded to climate change and initial human settlements, for example, on the islands of La Gomera (Canary Islands, Nogué et al., 2013) and São Nicolau (Cabo Verde, Castilla-Beltrán et al., 2020). Such analyses provide information on biodiversity baselines and trajectories of change after human colonization, both important to inform conservation management and policy and to understand the future direction of this biodiversity change (Bush et al., 2022; Castilla-Beltrán et al., 2020; Nogué et al., 2017; van Leeuwen et al., 2008; Willis & Birks, 2006).

We have compiled and integrated a global data set containing fossil pollen data for 29 islands covering the last 5000 years, plant census information for non-native species occurrences, and timing of human settlement. Using this data set, we investigate the timing, trajectory and magnitude of insular non-native vegetation abundance, with fossil pollen as the proxy. Across islands, we expect an increasing trend of non-native pollen towards the present. We expect the timing and magnitude of this increase to differ among individual islands, depending on individual human settlement histories.

MATERIALS AND METHODS

Study areas

Islands are well suited as study systems to reconstruct the vegetation history of non-native taxa as they represent isolated areas with discrete boundaries, and thus, the attribution of fossil pollen taxa to resident plant species is more straightforward than it is for mainland areas. In addition, fossil pollen time-series from isolated island systems contain low percentages of pollen taxa derived from long-distance transport (e.g. ±1.2% on Marion Island, Scott & van Zinderen Barker, 1985; or 3–5% in the Galápagos Islands, van der Knaap et al., 2012). This study focuses on 29 generally small islands worldwide that range from true oceanic islands ($n = 24$; 0.23–2040 km^2), some in archipelago settings (e.g. Gran Canaria, Tenerife and La Gomera in the Canary Islands), to other islands of volcanic origin and continental islands ($n = 5$; 2–102,387 km^2; e.g. Tawhiti Rahi, New Caledonia; Table S1). Human arrival falls within the period covered by most of the investigated time-series, allowing us to trace the transition of pollen composition from natural dynamics into human-dominated island systems.

Data acquisition and preparation

For each island, we assembled fossil pollen data from radiocarbon-dated sedimentary sequences, up-to-date plant species checklists and complementary literature comprising status information of species (native, non-native; Figure 1, Table S1). The cores were collected from a variety of environments (e.g. crater bog on Pico, Azores; swamp on Ha'afeva, Tonga; see sources listed in Table S1).

Fossil pollen taxa are identified at different taxonomic levels because closely related species or genera can have morphologically similar pollen. For example, within the plant families Brassicaceae, Caryophyllaceae, Cyperaceae and Poaceae, pollen is morphologically indistinct and can often only be identified to family level (Faegri, 1989; Tweddle et al., 2005). In contrast, pollen grains from many plant genera can be identified to species, thus, the fossil pollen taxa range from species to genera or even family levels to accommodate the ability of palynologists to identify pollen grains to the highest taxonomic level possible.

The published sedimentary sequences from all islands included in this study were chronologically dated using, for example, radiocarbon dating techniques and by building age-depth models (see individual sources of fossil pollen data, Table S1). As calibrated and standardized age information for all sequences, we used published age-depth models calibrated according to IntCal20 (Reimer et al., 2020, northern hemisphere) and SHCal20 (Hogg et al., 2020, southern hemisphere) (see individual sources of pollen data in Table S1). For the sequence from Santa Cruz, additional ^{210}Pb dating was undertaken to account for high accumulation rates in the upper part of the peat core (Froyd et al., 2014). In this study, time is provided as calibrated (cal.) years BP, using 1950 CE as year zero (Walker et al., 2009; cut-off sensu Nogué et al., 2021). We focus on the last 5000 cal. year BP. According to current information
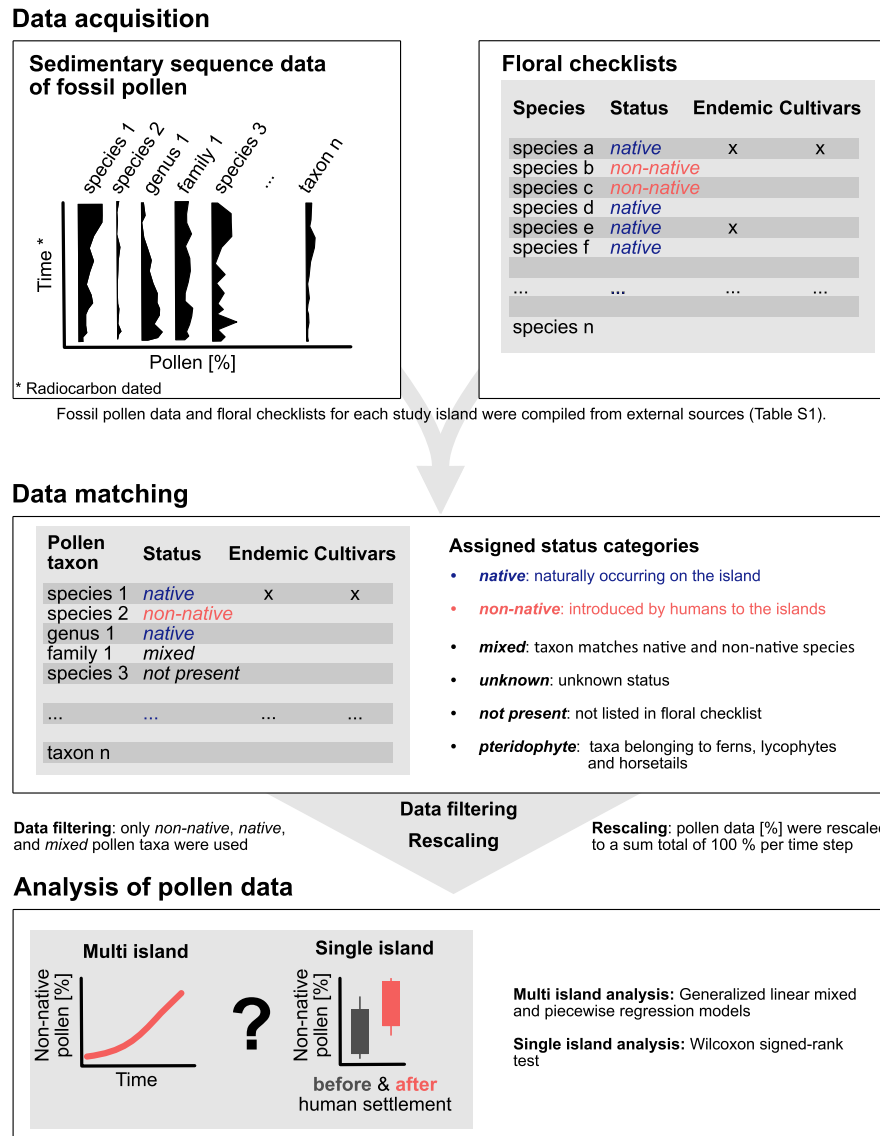
Data acquisition

Sedimentary sequence data of fossil pollen

Pollen [%]

* Radiocarbon dated

Floral checklists

Species	Status	Endemic	Cultivars
species a	*native*	x	x
species b	*non-native*		
species c	*non-native*		
species d	*native*		
species e	*native*	x	
species f	*native*		
...	...	...	...
species n			

Fossil pollen data and floral checklists for each study island were compiled from external sources (Table S1).

Data matching

Pollen taxon	Status	Endemic	Cultivars
species 1	*native*	x	x
species 2	*non-native*		
genus 1	*native*		
family 1	*mixed*		
species 3	*not present*		
...	...	...	...
taxon n			

Assigned status categories

- *native*: naturally occurring on the island
- *non-native*: introduced by humans to the islands
- *mixed*: taxon matches native and non-native species
- *unknown*: unknown status
- *not present*: not listed in floral checklist
- *pteridophyte*: taxa belonging to ferns, lycophytes and horsetails

Data filtering: only *non-native*, *native*, and *mixed* pollen taxa were used

Data filtering

Rescaling

Rescaling: pollen data [%] were rescaled to a sum total of 100 % per time step

Analysis of pollen data

Multi island

Non-native pollen [%]

Time

?

Single island

Non-native pollen [%]

before & **after** human settlement

Multi island analysis: Generalized linear mixed and piecewise regression models

Single island analysis: Wilcoxon signed-rank test

FIGURE 1   Schematic flow chart describing data acquisition, matching and analysis. The methodology developed aims at combining long-term fossil pollen data at variable levels of taxonomic resolution with biogeographic status information (*native*, *non-native*) of extant island floras as derived from checklists to gain insights into palaeoecological trends of non-native vegetation on 29 islands globally.

available, few remote islands were colonized before this date, given constraints on ocean voyaging technology (Leppard et al., 2022).

For all islands, we collected up-to-date checklists of vascular plant species that include information on the biogeographic status (*native* and *non-native*; written in italics if referring to status categories in the data set) of extant island floras (see Table S1). For islands in archipelago settings (e.g. Azores, Canary Islands), plant species checklists at archipelago level were used. Infraspecific taxa such as subspecies or varieties were disregarded, and hybrids were excluded from the analyses. It is important to highlight that plant species extinctions prior to checklists (mostly due to human encroachment) might not have been documented. Therefore, additional palaeoecological and botanical literature on known extinct or extirpated native plant taxa was used to complement

extant plant species checklists (e.g. *Quercus* sp. in Canary Islands, de Nascimento et al., 2009; *Notanthera heterophylla* on Alexander Selkirk and Robinson Crusoe, Stuessy et al., 2017; *Stachytarpheta fallax* on Cabo Verde; Romeiras et al., 2016; see sources listed in Table S1). The categories used to describe the biogeographic status of plant species (e.g. 'indigenous', 'native', 'invasive' and 'possibly non-native') differed among checklists. To overcome this inconsistency, we reduced the different categories to just two: *non-native* and *native*, based on whether a plant species was associated with human presence on an island (*non-native*) or not (*native*). The *native* category also included extinct native taxa.

To match fossil pollen taxa which refer to different extant plant taxa at species, genus or family level with the extant plant species checklist data, we used three steps (Figure 1):

1. *Matching*: To attribute biogeographic status levels from extant checklists of vascular plant species to the pollen (and spore) taxa, we assigned six categories: (i) *Pteridophyte* (spore-producing; belonging to ferns, lycophytes or horsetails), (ii) *non-native* (introduced by humans to an island), (iii) *native* (naturally occurring on an island), (vi) *mixed* (pollen matching both native and non-native species), (v) *unknown* (status not provided in the plant species checklist) and (vi) *not present* (taxon was not represented in the plant species checklist). Matching was done manually by comparing single pollen taxa with all species of the corresponding extant plant species checklist or, for extinct plant taxa, relevant literature. To attribute the status categories, we first matched pollen taxa at species level with the species occurring on the respective islands. In the second step, pollen taxa at genus and family levels were matched with all species from the island flora belonging to the corresponding genus or family respectively. For non-matching taxa, taxonomy and nomenclature were checked manually for synonyms in Plants of the World Online (POWO, 2022). If all species from the corresponding genus or family had the same biogeographic status (i.e. all being either *native* or *non-native*), we assigned this status level to the corresponding pollen type. As an example, on the Galápagos Islands, the pollen type *Scalesia* corresponds to a genus of the same name. The pollen is therefore classified as *native*, as all species of the genus reported from the Galápagos are native to the archipelago. In the same archipelago, the pollen type *Cinchona* is considered *non-native* as it matches only with a plant species that is non-native on the islands (Froyd et al., 2010). If a pollen type at genus or family level was matched with both native and non-native species of an island flora, it was assigned to the category *mixed*.

2. *Filtering*: This article is based only on pollen taxa and therefore spore-producing taxa classified as *pteridophytes* were not included in the final data set. Their sexual reproduction and dispersal strategy leads to the massive production of spores as propagules that could likely mask patterns of other less abundant pollen grains. Pollen taxa classified as *unknown* were discarded as their status was unclear. If pollen was classified as *not present* in the current island flora, it was excluded from the analysis as it most likely represented long-distance dispersal or represented unknown extinct island taxa. The final data set comprised only fossil pollen data with the assigned biogeographic status levels *native*, *non-native* and *mixed*.

Six islands (i.e. Hispaniola, Iceland, La Gomera, New Caledonia, Nightingale Island and Robinson Crusoe) were excluded from further analyses. This was done because the pollen data of these islands contained taxonomically poorly resolved or largely uncategorizable pollen taxa which hampered the assignment of *native* and *non-native* taxa (Table S1, Figure S1). Additionally, we excluded pollen data from Foa and Ha'afeva (Tonga) from further analysis, as the stratigraphic data had a very low temporal resolution (Figure S2). Thus, the final data set used here derived from 21 islands and 14 archipelagos and comprises percentage data for *non-native, native and mixed* pollen at discrete timesteps of varying length from records of up to 5000 cal. years BP. The data set represents a total of 665 plant taxa.

3. *Rescaling*: After filtering, the data set was rescaled to allow for an analysis of relative changes in non-native plant abundance on islands using two different approaches. In the first, the count or percentage data of *non-native*, *native* and *mixed* pollen grains was rescaled to 100% per time step (data set$_{lower}$). In a second approach, only the data of *non-native* and *native* pollen grains were used for rescaling (data set$_{upper}$). Pollen taxa classified as *mixed*, comprising both native and non-native taxa, are likely to represent more native taxa in early settlement periods. Therefore, the consideration of both scaling approaches provides the opportunity to analyse the upper (not considering pollen classified as *mixed*) and lower (including pollen classified as *mixed*) boundaries of non-native pollen abundances on islands.

Data on *endemic* and *cultivar* pollen were also considered, as *endemic* species are often negatively affected by human encroachment (e.g. displacement by non-natives), and *cultivar* species represent a subcategory of non-native species directly used by humans. We therefore marked *endemic* pollen taxa (i.e. native taxa limited to an island or archipelago) and *cultivars* (e.g. *Zea mays*), following the same procedure as described in data matching step 1. The information was taken from the extant plant species checklists (Table S1). Here, no rescaling was applied, and the data are presented as raw percentage data of the entire sedimentary sequence.

The onset of permanent human settlement on each island was retrieved from a range of archaeological sources to provide complementary environmental information for subsequent analysis (sources listed in Table S1).

Analysis

Data were analysed both jointly for all islands (multi-island analysis) and separately for each island (single-island analysis; Figure 1). Analysis and visualization were performed with the R software (R Core Team, 2022). All 21 islands with successful matching procedures and sufficient temporal resolution (i.e. minimum 25 total records and minimum five records per millennium) were included in the multi- and single island analysis.

All multi-island analyses were applied to data set$_{upper}$ and data set$_{lower}$ to account for the upper and lower limits

in non-native vegetational change. Trajectories of non-native pollen in time were visualized using local polynomial regression fitting. To analyse overall non-native pollen trajectories in time, three methods were applied.

a. A linear mixed effect model (LMM) was fit by restricted maximum likelihood using the *lme4* package (*lmer* function; Bates et al., 2015) to reveal temporal patterns of non-native pollen (as a proxy for the abundance of non-native vegetation) in time. Sums of non-native pollen per timestep were included simultaneously from all 21 islands with successful matching. Time (cal. years BP) was set as a fixed effect and islands additionally included as a random effect. The response variable was log-transformed to meet the requirements of a linear model and the residuals were checked for normal distribution to ensure goodness of fit.

b. Additionally, a piecewise regression model (using a Bayesian information criterion) was fit to the data with the package *segmented* (*segmented* function; Muggeo, 2017) to extract break points and abrupt changes in non-native pollen trajectories. This analysis was limited to the last 2000 cal. years BP, as for this time frame, the data resolution was best and single island sequences overlapped the most (Figure S3).

c. To link percentage data of non-native pollen (and thus the abundance of non-native vegetation) with taxonomic richness, we calculated the correlation (Pearson's r) of the percentage of native pollen and number of pollen taxa per time step jointly for all islands.

As complementary analyses, the overall trend of *endemic* and *cultivar* pollen in time was analysed using LMMs, applying the same model settings as presented above. The analysis was limited to timesteps where cultivar or endemic pollen was represented and for *cultivar*, pollen is presented only for the last 2000 cal. years BP due to limited data (Figure S3).

To put single islands trajectories in the context of individual human settlement histories and quantify magnitudes of change, the percentage of non-native pollen before and after human settlement was compared using Wilcoxon signed-rank sum tests. Trajectories of non-native pollen in time were visualized using a moving window approach (means of 250 years are shown) and boxplots.

RESULTS

We found substantial changes in the abundance of non-native vegetation on islands through time as expressed by their proportion of pollen (LMM $p < 0.001$, Table S2). When all 21 islands are analysed jointly, pollen values of taxa assigned to non-native flora show a tendency to increase starting ca. 1000 cal. years BP for both, upper and lower limit scenarios (Figure 2a). We identified break points at 102 cal. years BP (data set$_{upper}$) and 575 cal. years BP (data set$_{lower}$) before which the percentage of non-native pollen amounted to an average of 2% to 7% and after which these percentages reached 5% to 19% (Figure 2b, Table S2 & S3). This trend shows no sign of a deceleration towards the present.

The percentage of non-native pollen and the number of non-native pollen taxa was correlated with 0.5 (data set$_{lower}$, Pearson's r and $p < 0.001$) and 0.4 (data set$_{upper}$, Pearson's r and $p < 0.001$; Figure 2c). The percentage of pollen from endemic taxa decreases almost continuously towards the present (LMM, $p < 0.001$; Table S4, Figure S4a). Cultivar pollen abundance decreases faster towards the present compared with endemic pollen abundance (LMM, $p < 0.001$; Table S5, Figure S4b).

The timing, trajectory and magnitude of change in non-native pollen varies substantially between islands across the data set (Figure 3). Specifically, most islands show an increasing trend of non-native pollen over time that starts with the onset of human settlement (i.e. Flores, Great Mercury, Mo'orea, Raivavae, Rimatara, São Nicolau, Tawhiti Rahi and Tristan da Cunha). Besides a post-settlement increase in non-native pollen, several islands exhibit an increasing trend in non-native pollen slightly before the onset of human settlement (i.e. Alexander Selkirk, Brava, Gran Canaria, Maui, Mauritius, Pico, Rapa Iti, San Cristóbal and Santa Cruz). In addition, three islands show trends without clear directionality (i.e. Santo Antão, Tenerife and Uta Vava'u). Finally, for Vanuatu, only post-settlement fossil pollen data were available and a comparison with pre-settlement times was not possible. Still, the island shows an increase of non-native pollen towards the present. In total, 14 islands exhibit significantly more non-native pollen post-settlement compared to pre-settlement times. The patterns were similar for data set$_{lower}$ and data set$_{upper}$ (see Figure S5). On average, the islands recorded 1–6% non-native pollen preceding permanent human settlement and 5–16% non-native pollen after the onset of human settlement history (based data set$_{lower}$ and data set$_{upper}$ respectively). The percentage values of non-native pollen taxa for all islands increases towards the present, reaching average values of 8–25% (based data set$_{lower}$ and data set$_{upper}$ respectively). The magnitudes of non-native pollen on islands during human settlement times vary from below 5% (i.e. Rapa Iti, Tristan da Cunha) to more than 20% (i.e. Alexander Selkirk, Gran Canaria, Mo'orea and Raivavae).

DISCUSSION

Palaeoecological data reveal an increasing trend in non-native pollen proportions on islands globally starting approx. 1000 cal. years BP and continuing to increase
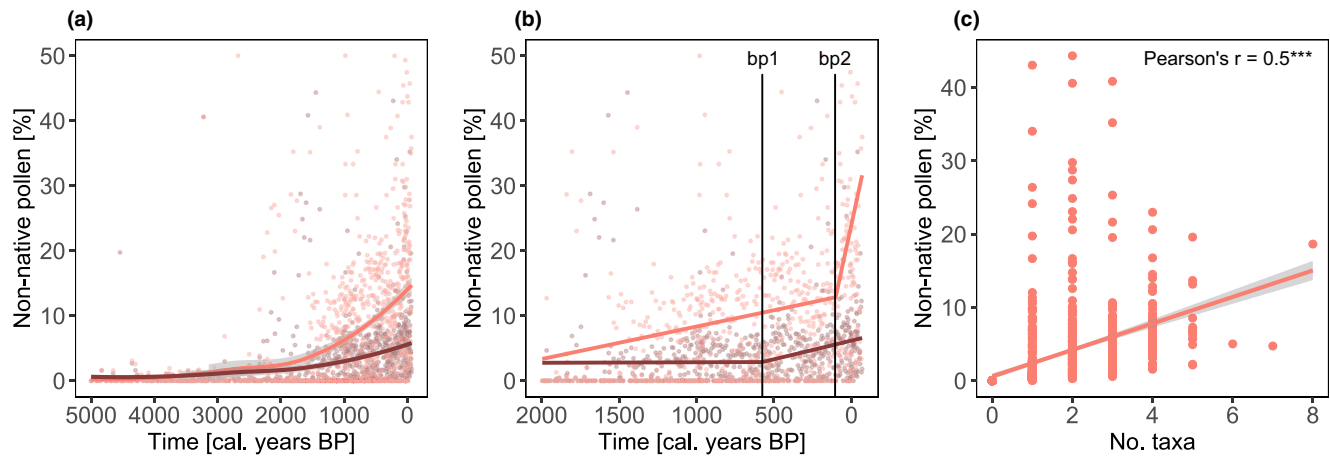
FIGURE 2 (a) Percentage of pollen of non-native vegetation for the past 5000 calibrated years Before Present (cal. years BP) for 21 islands, represent the maximum (light red, data set$_{upper}$) and minimum (dark red, data set$_{lower}$) limits of non-native vegetation abundances. For trend visualization, a local polynomial regression was fitted with a 95% confidence interval (cut-off at 50% non-native pollen, outliers are not shown). (b) Pollen of non-native vegetation for the last 2000 cal. years BP, showing piecewise regression models (using Bayesian information criterion) of non-native pollen in time (cal. years BP) with resulting break points at 575 (break point 1, bp1) and 102 (break point 2, bp2) cal. years BP (cut-off at 50% non-native pollen, outliers are not shown). Scale is limited to 2000 cal. years BP. (c) To investigate if pollen abundance translates into species richness, the percentage of non-native pollen was regressed against the number of pollen taxa during each time step and for all 21 islands (Pearson's $r = 0.5$, $p < 0.001$, based on data set$_{lower}$).

towards the present. The analysis of single islands shows that the onset of non-native vegetation and their magnitude of change differ among islands. This is likely related to the individual human settlement histories of these islands. Using pollen of non-native plant species as proxies for the abundance of non-native species translates into substantial vegetational changes due to human-mediated species introductions.

This increase in non-native vegetation during the last millennium diverges from currently available global data sets based on published first records of non-native species. Most of these records focus on the past 500 years, with reliable data largely being constrained to the last 200 years (Seebens et al., 2017; global, not specific to islands). The temporal divergence between palaeoecological trends of non-native plants presented in this article and the published scientific written records indicates that advances in the understanding of the dimensions, importance and impacts of long-term biodiversity change caused by non-native plants on islands can be fostered by palaeoecological data. In addition, we found that towards the present 8–25% of pollen grains may be attributed to non-native plant taxa. Although pollen percentages reflect plant abundances only indirectly (e.g. due to palynologically silent taxa or differing pollen productivity, Birks & Birks, 1980), this increase in non-native vegetation underlines the scale of human-mediated species' introductions and the potential impact they may have on islands. Importantly, these biodiversity changes seem accelerated towards the present. In addition, previous studies have demonstrated that plant species richness is reflected in pollen taxonomic richness (Birks et al., 2016) and the positive relationship in our data (Figure 2c) appears to confirm this for islands as

well. Most likely, increasing abundance of non-native vegetation is the result of both ongoing introductions and expansions of present non-native species. Differences in pollen productivity between species might also hamper a higher correlation between non-native pollen percentages and the number of taxa.

Anthropogenic forces add another layer to the ever-changing nature of islands and have relatively recently (in geological timescales) emerged as dominant drivers in ecological systems (Fernández-Palacios et al., 2021). As the result of numerous human-mediated introductions of non-native species, novel species assemblages and ecosystems have established on islands globally (e.g. Russell & Kueffer, 2019). For example, the sweet chestnut (*Castanea sativa*) forests on La Palma (Canary Islands), initially planted for agricultural purposes, are increasingly replacing parts of the laurel forest, naturally dominated by Macaronesian-endemic species, such as *Ilex canariensis*, *Laurus novocanariensis* or *Persea barbujana* (Beierkuhnlein et al., 2021; Devkota et al., 2020). In the Galápagos Islands, large blackberry (*Rubus niveus*) or guava (*Psidium guajava*) populations are thriving where once endemic species (e.g. *Scalesia pedunculata* on Santa Cruz) were dominant (Urquía et al., 2019; Walentowitz et al., 2021). Our findings open a new perspective on the timing of the development and the extent of novel species assemblages that seem to emerge up to 1000 years earlier than historical records suggest. Furthermore, our results contribute to the discourse on the naturalness of extant island biodiversity around questions like what can be considered as 'natural' island biodiversity if non-native vegetation started to increase about one millennium ago? Our results demonstrate the power of long-term palaeoecological records that extend beyond the written
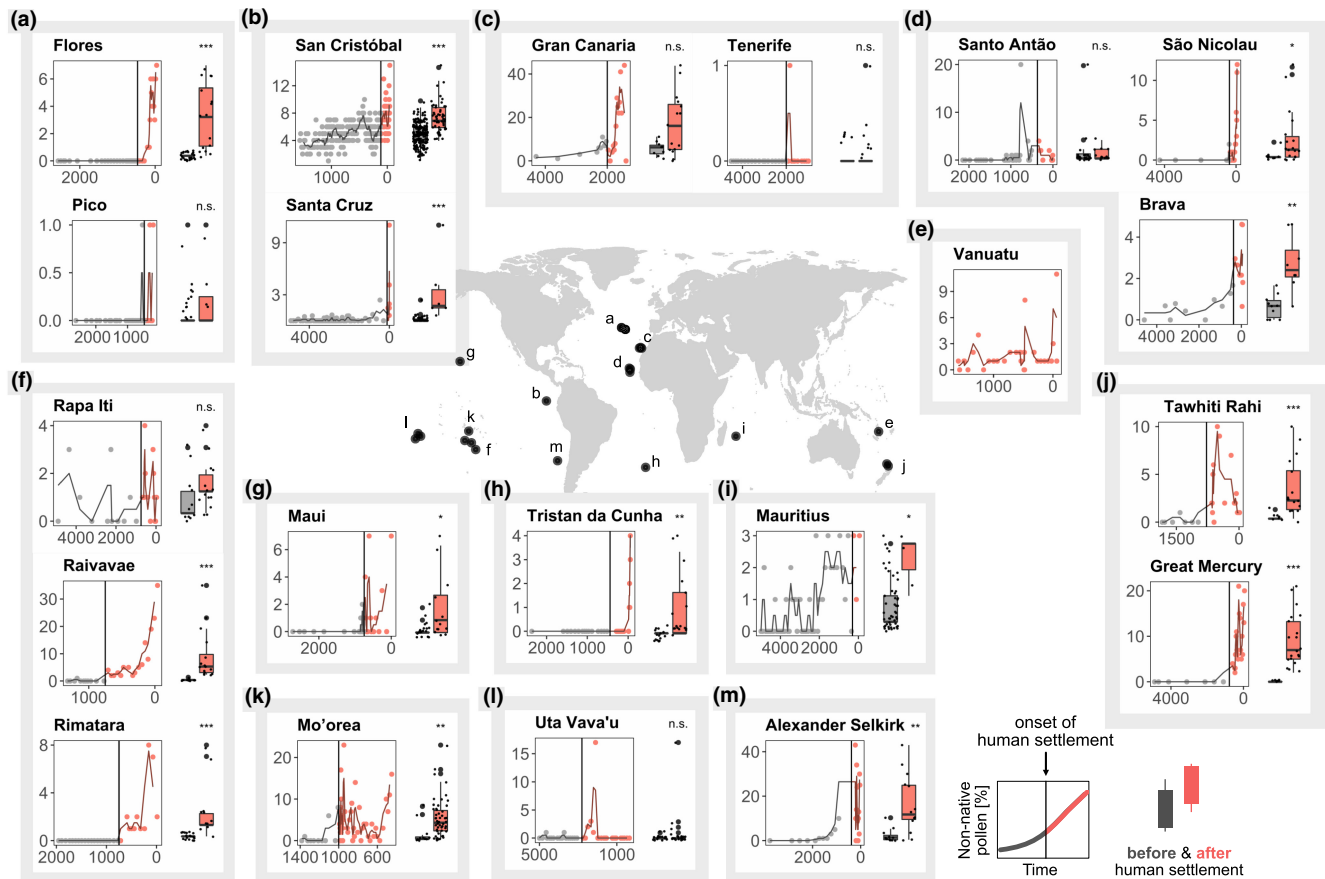
FIGURE 3 A total of 5000 calibrated years Before Present of trajectories of non-native pollen for 21 islands globally. The onset of human settlement is indicated by a black vertical line. A comparison of non-native pollen taxa (%) before and after human settlement is provided as boxplots. Significance levels are indicated by asterisks (Wilcoxon signed-rank sum tests). Colours in grey correspond to data points before and colours in red to data points after human settlement. Plot legends are provided at the bottom-right. Note that for Vanuatu, pollen data are only available for a time frame after human settlement, and consequently, no comparison of non-native pollen before and after the human settlement is possible. Figures are based on data set$_{lower}$ and results for data set$_{upper}$ presented in Figure S5. Note furthermore that on Rapa Iti, patterns in non-native pollen before human arrival can most likely be attributed to contamination with *Pinus* pollen at the coring site (Prebble et al., 2019).

record and observations to help distinguish between natural patterns and those affected or caused by non-native vegetation, and ultimately by human encroachment.

Our findings support the notion of the *Hookerian* shortfall, as the botanist Joseph Dalton Hooker already raised the question in the nineteenth century of how islands can be considered as 'natural laboratories' in light of the impacts of human activities (Carine & Menezes de Sequeira, 2020). An example from the Galápagos Islands illustrates this shortfall: According to our findings, non-native vegetation accounted for about 6–9% of their flora by the time Charles Darwin visited the archipelago in the year 1835. Thus, even Charles Darwin most likely visited an archipelago where novel plant communities were already present, and the flora had in addition to the introduced non-native plants been impacted by the removal and inter-island translocation of tortoises by whalers and the introduction of non-native herbivores (Bush et al., 2022). The human-influenced nature in the Galápagos Islands continues to influence conservation management in the archipelago, which does not fully

consider the long-term perspective on change in species compositions (Bush et al., 2022). This example illustrates how information on the temporal abundance and trajectories of non-native vegetation, determined through palaeoecological data, is required to determine the degree of naturalness of island vegetation, facilitate the establishment of baseline information and to identify introduced taxa (e.g. Bush et al., 2014; Gillson, 2022; van der Knaap et al., 2012). Especially on islands, where expensive conservation and restoration efforts are being undertaken to preserve native biodiversity and recover unique ecosystems (e.g. Jones et al., 2016), the establishment of such baselines is imperative to inform such efforts (Barak et al., 2016; Bush et al., 2022; Nogué et al., 2017; Willis & Birks, 2006).

Despite non-native species being currently omnipresent and widespread in island systems globally (Essl et al., 2019), the timing of introduction and trajectories of their expansion differ substantially between islands and archipelagos. Here, we use the onset of human settlement to explain differences in trajectories. For a widely

dispersed suite of islands, namely Flores, Great Mercury, Mo'orea, Raivavae, Rimatara, São Nicolau, Tawhiti Rahi and Tristan da Cunha, the onset of rising trends in non-native vegetation coincides with the onset of permanent human settlement in the islands. Similar trajectories are exhibited by Alexander Selkirk, Brava, Gran Canaria, Maui, Mauritius, Pico, Rapa Iti, San Cristóbal and Santa Cruz, but with the difference that these nine islands show increasing trends in non-native vegetation before the onset of human settlement. This divergence might be attributed to impacts by known earlier presences of people before permanent settlement, or it could mean that more robust chronological data is required for the initial human colonization period. In Galápagos, permanent settlement on the islands occurred comparatively late in human history (Tye, 2006). While the archipelago had already been discovered in 1573 AD, the scarcity of freshwater hampered permanent colonization. Nevertheless, earlier occasional visits by pirates, mariners and whalers impacted the vegetation by both accidentally and intentionally introducing non-native species long before the onset of permanent settlements in the nineteenth century (Bush et al., 2022). Furthermore, pollen records from islands that were never permanently settled but temporarily exploited by humans for resources have also revealed plant introductions, such as the subantarctic Auckland Islands, demonstrating the sensitivity of the method (Wilmshurst et al., 2015). In addition to human-mediated introductions, it is important to consider other environmental factors, such as legacies of land-use change, local extinctions of species, ecological cascading effects or ecosystem conversion by introduced mammals. These are just some examples of potential drivers considered to be causing increases in non-native plant species (Anderson et al., 2011; Bush et al., 2022; Castilla-Beltrán et al., 2020; Fernández-Palacios et al., 2021; Kueffer et al., 2010; Prebble et al., 2019). Furthermore, interrelations between natural forces, such as climate change (e.g. de Boer et al., 2013) and volcanic impacts (Castilla-Beltrán et al., 2021, 2023) with human history could be of interest.

Mismatches between settlement dates and onsets of the rise of non-native vegetation or non-directional changes in non-native pollen percentages might, besides island characteristics or the presence of people before permanent settlement, also be attributable to data and methodological limitations. Inaccuracies and uncertainties in radiocarbon dating might be one potential reason for mismatches, differences in pollen source area resulting from variability in depositional environments and the type and size of coring sites, for example, small bogs to large lakes (Jacobson & Bradshaw, 1981) may also influence early detection of the presence of non-native species in our records (see Table S1). Inadequate pollen grain identification or inaccurate assessment of species' status (e.g. native or non-native) in botanical checklists (e.g. van Leeuwen et al., 2008) are additional

pitfalls. In this article, we demonstrate that while pollen identification issues are a source of uncertainty, the palaeoecological data quality on the attribution of species as native or non-native is constantly increasing (Coffey et al., 2011; van Leeuwen et al., 2008). Additionally, our analysis is driven by pollen taxa that were clearly attributable as non-native (see methods). This constrained any insights being gained from large and biodiverse islands (e.g. Hispaniola, New Caledonia) for which our matching procedure resulted in coarse categories, but it provides a robust and rather conservative estimate of the phenomenon. Coarse taxonomic resolution might also be the reason we observed trends without clear directionality for Santo Antão, Tenerife and Uta Vava'u. In New Zealand (Sutton et al., 2008), Cook Islands (e.g. Kirch & Ellison, 1994; Sear et al., 2020) and Rapa Nui (Rull, 2016), cases have been made for earlier human contact than information obtained from archaeological evidence for human settlement, based on the putative presence of non-native pollen, or other palynological signatures. However, in the case of New Zealand, with the addition of more palaeoecological records and novel proxies with robust radiocarbon-dated chronologies (e.g. Wilmshurst et al., 2008), along with the large number of early archaeological sites with robust chronological information, these early claims are no longer supported by data (Wilmshurst et al., 2011).

Russell and Kueffer (2019) describe islands as microcosms in which we can observe biodiversity changes in the Anthropocene and can develop strategies to cope with these changes. In line with this, we have demonstrated the utility of fossil pollen data to improve existing biodiversity baselines on islands. Other proxy data have the potential to reveal similar global trends (e.g. for macroinvertebrate extinctions and introductions; Liebherr & Porch, 2015; Prebble et al., 2016). The temporal divergence between palaeoecological trends of non-native plants presented in this article and the published scientific written records indicates that little is known about the dimensions, importance and impacts of long-term biodiversity change caused by non-native plants on islands. In addition, our results support the idea that human impacts on islands may occur before permanent settlement (Bush et al., 2022; Raposeiro et al., 2021). However, it is still not well understood why some islands appear to be more impacted by these early introductions than others. Overall, our findings suggest that incorporating a long-term perspective into the management of non-native vegetation on oceanic islands will lead to more informed management decisions and robust conservation outcomes. Such information is much needed to contextualize ecological restoration and research related to novel ecosystems.

AUTHOR CONTRIBUTIONS

AW, MS and SN designed the study. AW, NS, ACB, JMFP, SB, SC, SGH, KJ, MP, JMW, CAF, EJB, LDN,

PEER REVIEW

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OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at: https://zenodo.org/badge/latestdoi/566995168.

DATA AVAILABILITY STATEMENT

All data and code are fully accessible via Zenodo: https://zenodo.org/badge/latestdoi/566995168.

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SUPPORTING INFORMATION

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

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