Genetic Origins of the Kiritimati Population from Central-Eastern Micronesia

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Abstract

The migration of Austronesian-speaking populations through Oceania has intrigued researchers for decades. The Kiribati islands, situated along the boundaries of Micronesia and Polynesia, provide a crucial link in this migration. We analyzed the genome-wide data of the Kiritimati population of Kiribati to uncover their genetic origins and connections with other Oceanian groups. Our study reveals that the Kiritimati population primarily exhibits Remote Oceanian-related ancestry associated with ancient Lapita and present-day Polynesian populations. In addition, our identity-by-descent analysis identifies populations from the coastal southern Philippines as their closest relatives in Island Southeast Asia. The genetic links between Kiritimati, ancient Lapita, and modern Polynesians underscore the shared ancestry and continuous gene flow across these regions. This genetic continuity and ongoing links are supported by linguistic and cultural evidence, illustrating a complex history of migration and admixture in Oceania.

Key words: population genetics, Oceania, Micronesia, Polynesia, Kiritimati, human history.

Significance

The genetic origins of Pacific Island populations are complex and have long been debated, particularly concerning the pathways and relationships between Micronesian and Polynesian groups. This study reveals that the Kiritimati population, previously underrepresented in genetic research, primarily shares ancestry with ancient Lapita people and modern Polynesians, with a closer genetic link to populations from the Philippines. These findings refine previous models and provide new insights into the migration routes and connections among Oceanian populations, enhancing our understanding of human movement and cultural exchange across the Pacific.

Introduction

Kiritimati, also known as Christmas Island, is the largest atoll in the world, spanning an area of 388 km^2. Situated in the central Pacific Ocean, Kiritimati is part of the Republic of Kiribati. When Europeans first visited during James Cook's expedition in 1777, the island was found uninhabited (Cobbe 1979). However, archaeological evidence, including radiocarbon dating, suggests that Polynesians inhabited

Kiritimati between 1250 and 1450 CE (Anderson et al. 2000). Following European contact, the island remained deserted until the 1920s when Gilbertese-speaking people from the Gilbert Islands arrived to work on coconut plantations. In the 1950s, Kiritimati saw a new influx of inhabitants as a contingent workforce for the British-American nuclear testing program. Following Kiribati's independence from the United Kingdom in 1979 (McIntyre 2012), further migrations to Kiritimati occurred, increasing its population and integrating the recent migrants into the socio-economic fabric of the newly independent nation. Presently, Kiritimati has a population made up of migrants coming from the various islands of the Girbertise Archipelago, and thus represents a proxy for the entire area.

The Gilbert Islands, of which Kiritimati is a part, belong to Micronesia, a subregion in Oceania that encompasses 2,000 small islands across three other archipelagos: the Caroline Islands, the Mariana Islands, and the Marshall Islands. Situated in the southeasternmost section of Micronesia, the strategic location of the Gilbert Islands makes it a critical interaction point for diverse populations from neighboring remote islands. The islands exhibit a rich history of interaction with other Polynesian and Micronesian groups, evident through archaeological, linguistic, and cultural evidence (Anderson et al. 2000; Macdonald 2001; Fischer 2002; Petersen 2009; McIntyre 2012). Cultural practices in the Gilbert Islands, such as traditional navigation, canoe building, and communal meeting houses, closely resemble those in Polynesian and Micronesian societies, suggesting a flow of knowledge and traditions. Historical accounts from European explorers and missionaries in the 18th and 19th centuries document trade relationships, intermarriage, and the movement of people between the Gilbert Islands and neighboring island groups, highlighting the interconnectedness of these communities.

The inter-island interactions underscore the dynamic nature of Pacific Island societies (Fischer 2002; Petersen 2009). Recent genetic studies portray the Micronesian region with a complex demographic history (Liu et al. 2022). At least five streams of migrations have been identified, four from branches of East Asian-related ancestry and one from an ancestry related to Papuans. These migrations include Marianas and Palauan-related ancestries appearing in western Micronesia before 2800 and 2400 BP, respectively; a Lapita-related ancestry appearing in central-eastern Micronesia before 1800 BP; and a Polynesian-related ancestry brought about by westward Polynesian migrations after 1000 BP. Consequently, the peopling of Micronesia is distinctively different in each region. In the west, the Palau and Marianas Islands were inhabited by migrants directly from Island Southeast Asia, likely coastal populations from the Philippines or eastern Indonesia. In the east, the islands of Chuuk and Pohnpei were inhabited by Lapita-related populations, either directly from Vanuatu or the western Polynesian islands of Samoa and Tonga.

Understanding the human past of the Gilbertese-speaking population of Kiritimati is crucial given its strategic location. However, the genetic origin and affiliations of this population remain largely limited (Palencia-Madrid et al. 2022). This study addresses this issue by investigating genome-wide autosomal markers of the Kiritimati population. Our goal is to elucidate the genetic structure of the Kiritimati population and explore how past migrations, admixture, and genetic drift have shaped the genetic landscape of this remote island community. By examining these genetic markers, we aim to provide a clearer picture of the historical and genetic influences that have contributed to the current genetic makeup of Kiritimati's inhabitants. This research not only fills a gap in our understanding of Kiritimati's human history but also contributes to the broader knowledge of Pacific Islander genetic origins and migration patterns.

Results

The Genetic Relationship Between Kiritimati and Asia-Pacific Populations

Following quality control, 19 out of 20 Kiritimati individuals were retained for merging with publicly available datasets. To give an overview of the population structure of Kiritimati in relation to worldwide populations, we ran a principal component (PC) analysis (Fig. 1b). Kiritimati exhibited clustering with Asia-Pacific groups, forming a distinct cline between East Asian and Australasian clusters, suggesting a history of admixture between two ancestries. Australasian is defined here as an ancestry shared by Papuans, Australians, and Southeast Asian Negritos (Larena, McKenna et al. 2021; Göllner et al. 2022). Restricting the PC analysis to East Asian and Oceanian groups (Fig. 1c), PC1 distinguished Austronesian-related versus Australasian-related ancestries, while PC2 highlighted Australasian versus Remote Oceanian-related ancestries. Notably, Kiritimati formed a distinct cluster adjacent to Remote Oceanian groups from the Society Islands, Marquesas, and central-eastern Micronesian groups of Chuuk and Pohnpei.

To delve deeper into the population structure of various Remote Oceanian groups, an unsupervised Admixture clustering algorithm was utilized (Fig. 2). At K3, clusters were characterized by Australasian-related ancestry (light orange component) and East Asian-related ancestry (blue component). At K5, Remote Oceanians established their unique dark blue component, evident in Society Island, Marquesas Island, and Kiritimati population groups. At K7, further differentiation occurred within Remote Oceanians, with Polynesian-related (light blue) and central-eastern Micronesian-related (dark blue) ancestries emerging.

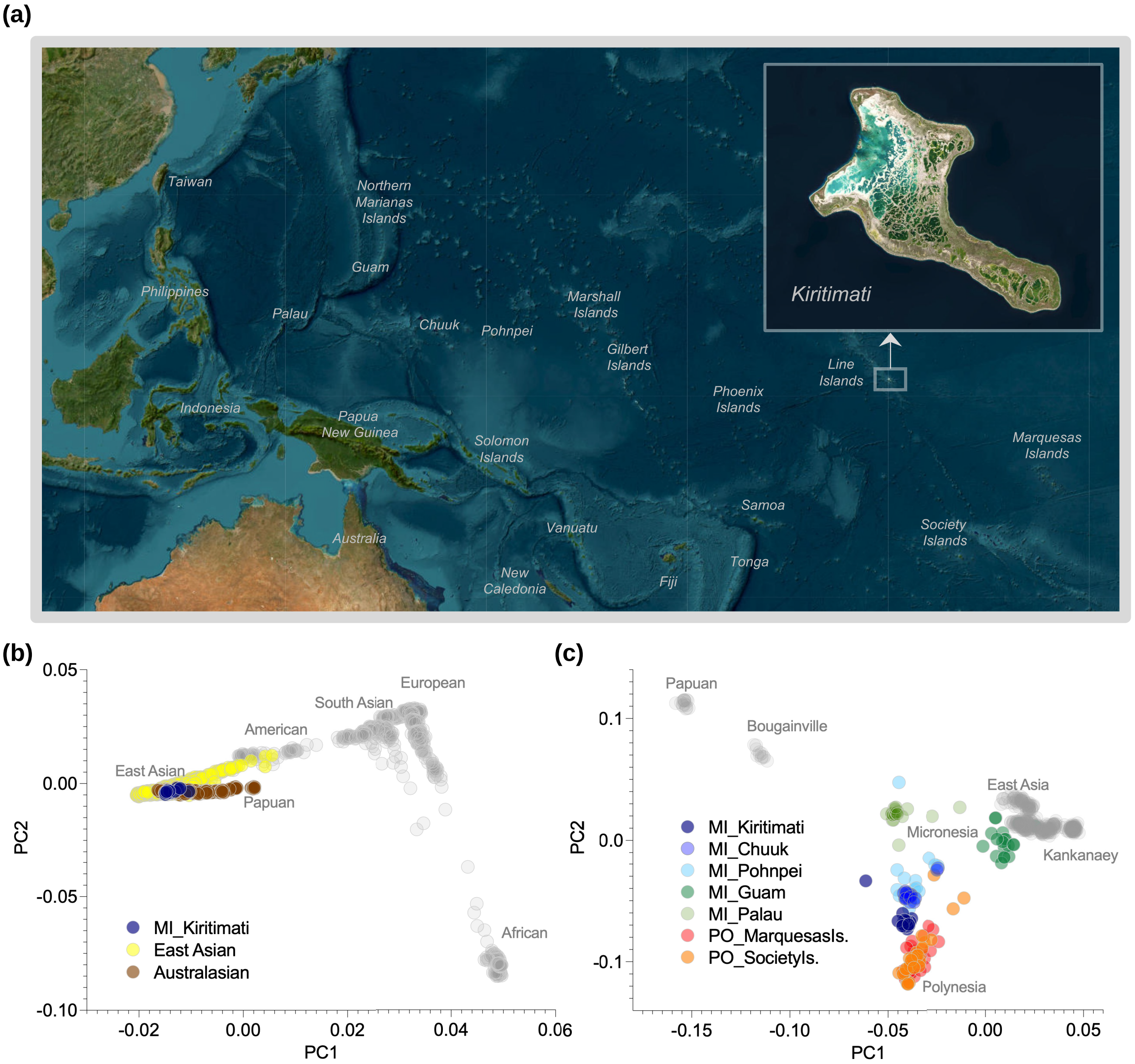

Fig. 1. Overview of population structure and genetic relationships of Kiritimati. a) Map of Oceania indicating the location of various island groups, with Kiritimati highlighted in an inset figure. Basemap: Esri World Imagery © Esri; map rendered using Leaflet. b) Principal component analysis of worldwide populations or c) restricted to Asia-Pacific populations. Colored circular markers represent specific populations or population clusters. MI, Micronesian; PO, Polynesian.

Kiritimati, as well as Chuuk and Pohnpei, displayed a notable proportion of the latter. On the other hand, Micronesians from the western region, Palau, and Guam, retained the blue component observed in coastal lowlander groups of the Philippines and other East Asian groups.

Kiritimati Islanders Share Ancestry with Eastern Micronesians and Polynesians

To identify the population with the highest genetic affinity with Kiritimati, we performed pairwise f2 and fixation index (FST) statistics in the form f2 (Kiritimati, X) and FST (Kiritimati, X). Kiritimati displays the closest genetic affiliation with Chuuk and Pohnpei populations, indicating a shared demography among central-eastern Micronesian groups (Fig. 3a to c). The results were consistent when we ran outgroup F3 statistics in the form f3 (Mbuti; Kiritimati, X), Kiritimati displays the highest shared genetic drift with Chuuk and Pohnpei populations (Fig. 3d).

The examination of genetic affiliations was extended through the application of the test f4(Mbuti, Kiritimati, Polynesia, Micronesia). This analysis aimed to identify

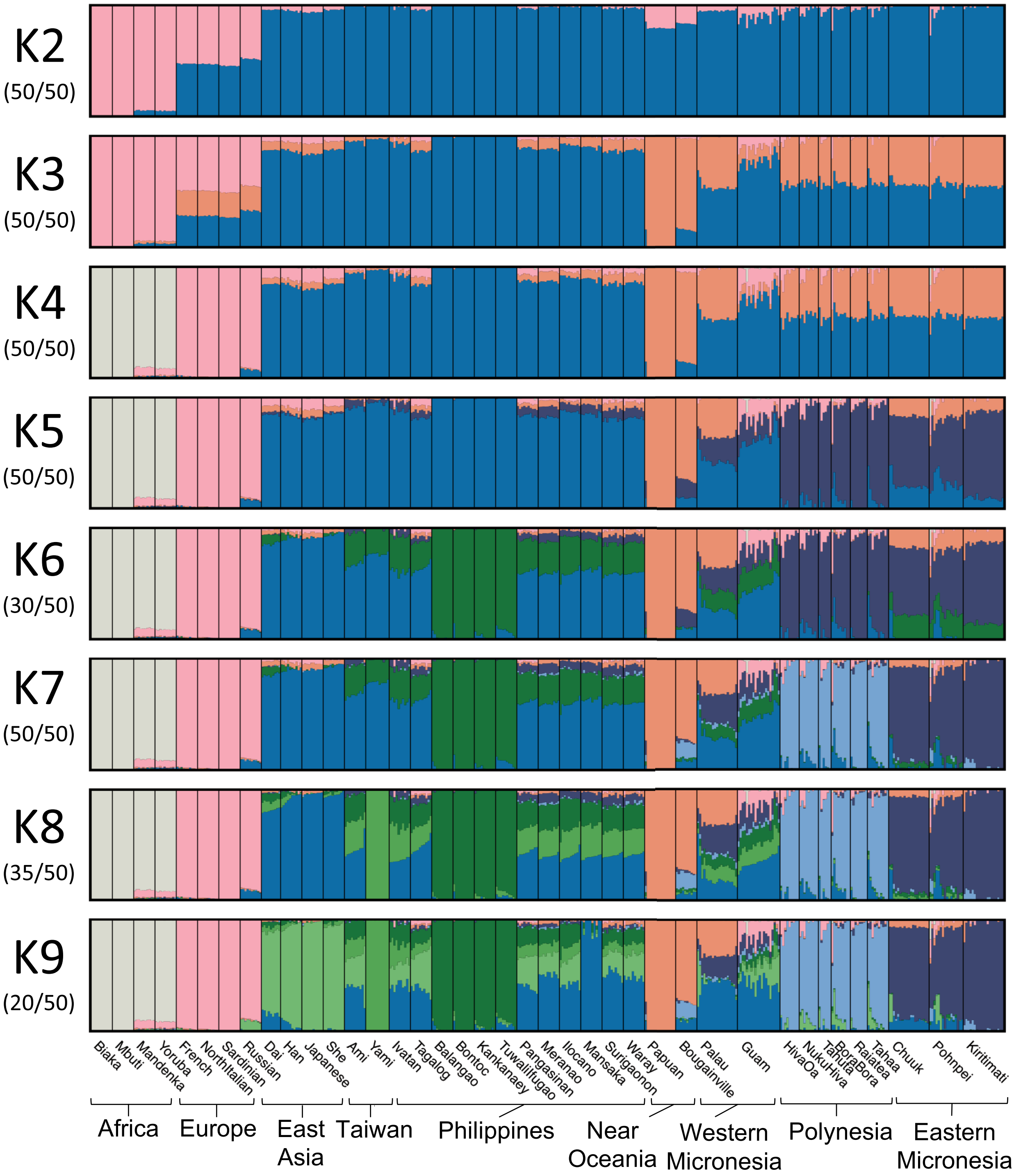

Fig. 2. Admixture analysis. Clustering of populations assuming K2 to K9 number of genetic ancestry components. The analysis was run for 50 iterations, with common modes of replicates for each K identified using CLUMPP. The predominant mode for each K was subsequently visualized using Pong v1.4.

whether Kiritimati exhibited a stronger genetic association with Polynesian groups (Society or Marquesas Islands) or Micronesian groups (Palau, Guam, Chuuk, or Pohnpei). In comparison to Society or Marquesas Island groups, Kiritimati demonstrated a closer genetic affinity with Chuuk and Pohnpei (supplementary fig. S1a and b, Supplementary Material online). This observation suggests a shared genetic history between Kiritimati and these Micronesian populations. Conversely, in contrast to Palau and Guam, Kiritimati exhibited a higher genetic affinity

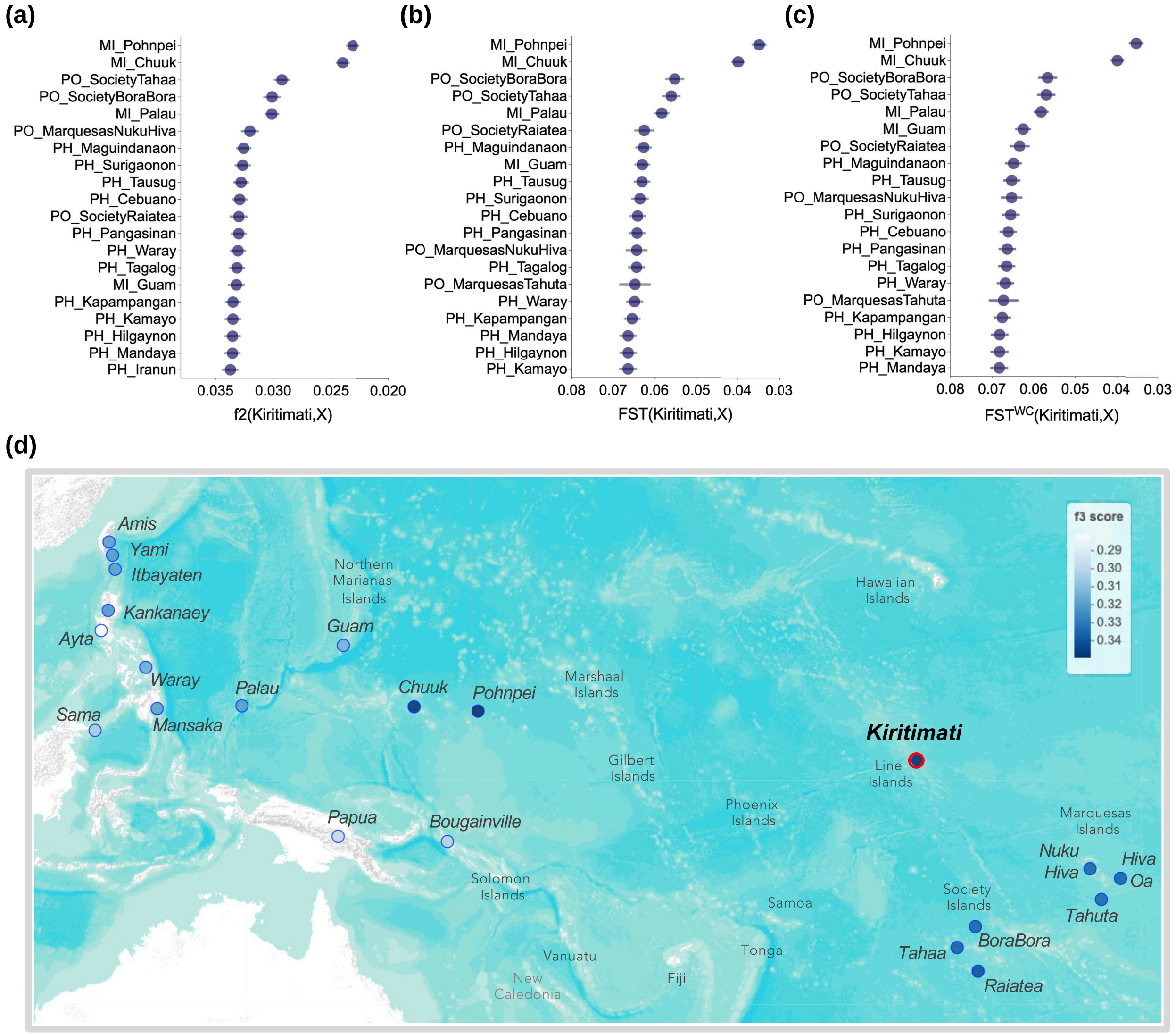

Fig. 3. Genetic affinities of Kiritimati. Levels of a) pairwise f2, b) Hudson's FST, and c) Weir and Cockerham's FST statistics indicate the top 20 populations with the highest genetic affinity with Kiritimati. Error bars represent 1.96 standard error of the estimate. d) Map of Oceania with the location of the top 20 populations represented by circular markers indicating the levels of shared genetic drift with Kiritimati based on outgroup F3 statistics in the form f3 (Mbuti; Kiritimati, X). Kiritimati is represented by the blue circular marker with red circular outline. The intensity of the blue gradient reflects the level of shared genetic drift (range: 0.28 to 0.35), with darker shades representing higher values. MI, Micronesian; PO, Polynesian; PH, Philippine.

with Society or Marquesas Island groups (supplementary fig. S1c and d, Supplementary Material online). This disparity indicates a distinct demographic history among Micronesian groups, with the central-eastern section of Micronesia, including Chuuk, Pohnpei, and Kiritimati, displaying a shared ancestry with Polynesians.

To explore the genetic relationships among various groups of the central-eastern section of Micronesia, we ran a combination of f4 tests between Chuuk, Pohnpei, and Kiritimati, using Mbuti as an African outgroup (supplementary fig. S1e to g, Supplementary Material online). Our findings indicate that Chuuk and Pohnpei exhibit a higher degree of shared ancestry with each other. Relative to Kiritimati, Chuuk, and Pohnpei form a clade together, indicating a closer genetic relationship between these two Micronesian groups.

To identify if there is gene flow between Kiritimati and Polynesian populations, we utilized the test f4(Mbuti, Polynesia; Chuuk/Pohnpei, Kiritimati). We find Kiritimati to have excess allele sharing with populations from the Society and Marquesas islands (supplementary fig. S1h to m, Supplementary Material online). This Polynesian genetic signal is ancestral to both Society and Marquesas Island groups, given that Kiritimati is equidistant to both

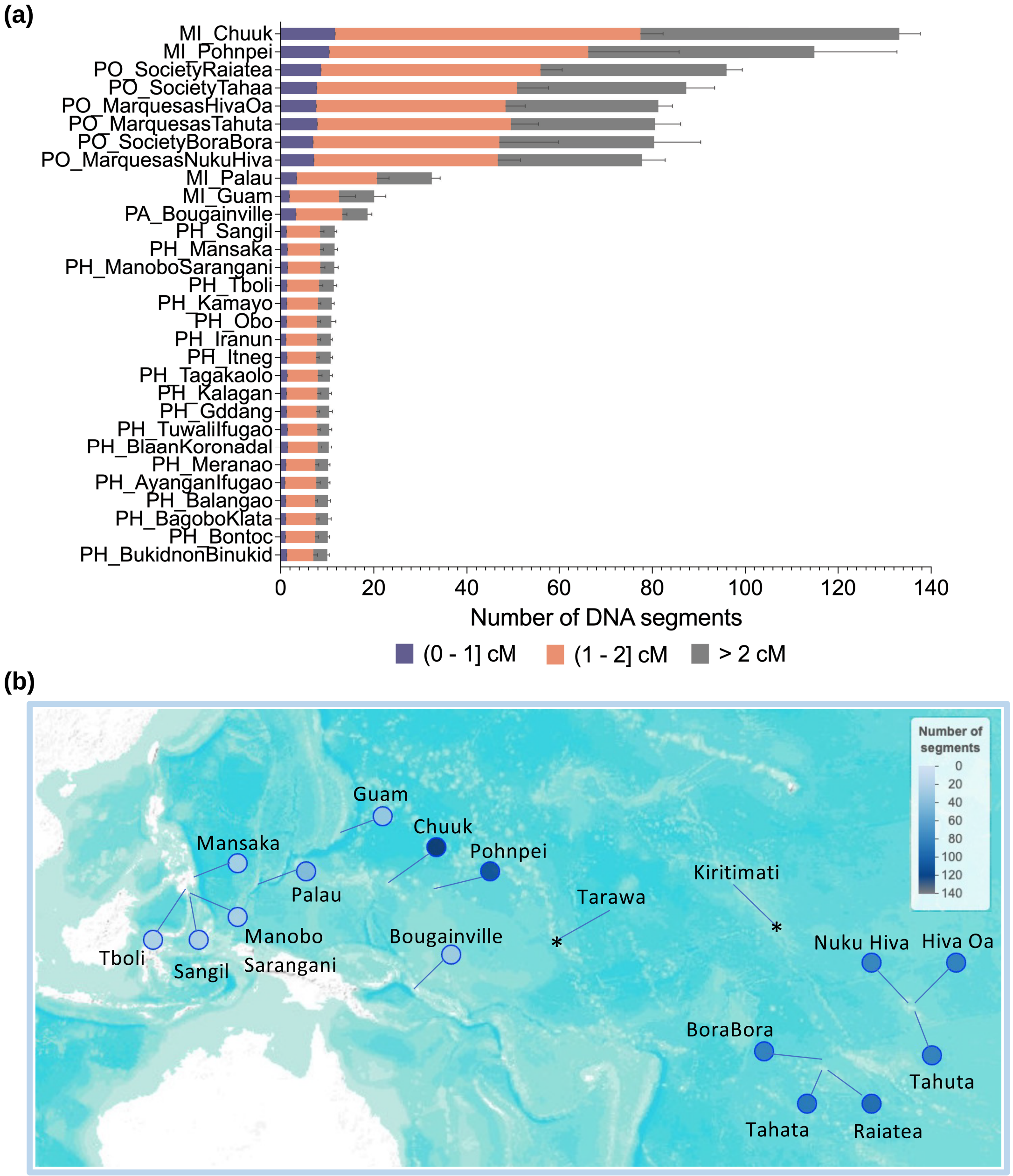

Fig. 4. IBD sharing with Kiritimati. a) Sharing of DNA tracts that are identical by descent with Kiritimati, top 30 populations. Numbers on the bars reflect the count of DNA segments of the corresponding length category, and error bars represent 95% confidence interval. b) Map of Oceania showing the location of the top 15 populations with circular markers indicating the levels of IBD sharing with Kiritimati. The intensity of the blue gradient reflects the level of IBD sharing with Kirtimati, based on the total number of shared segments (range: 11 to 133), with darker shades representing higher values. Asterisks represent the location of Kiritimati and Tarawa of the Gilbert Islands. MI, Micronesian; PO, Polynesian; PH, Philippine.

Society and Marquesas when we use the test f4(Mbuti, Kiritimati; Society Tahaa, Marquesas Nuku Hiva or Hiva Oa) ($Z = -0.0002$).

We extended further our investigation and utilized a haplotype-based analysis as a complementary method to determine the genetic affiliation of the Kiritimati population (Fig. 4; supplementary table S1, Supplementary Material online). Consistent with the earlier results, Kiritimati shares the highest number of IBD (Identity by Descent) segments with central-eastern Micronesians, Chuuk, and Pohnpei, at various length categories. They also share higher number of shared IBD with Polynesian groups from Marquesas and Society Islands relative to the western Micronesian groups of Palau and Guam. Among the

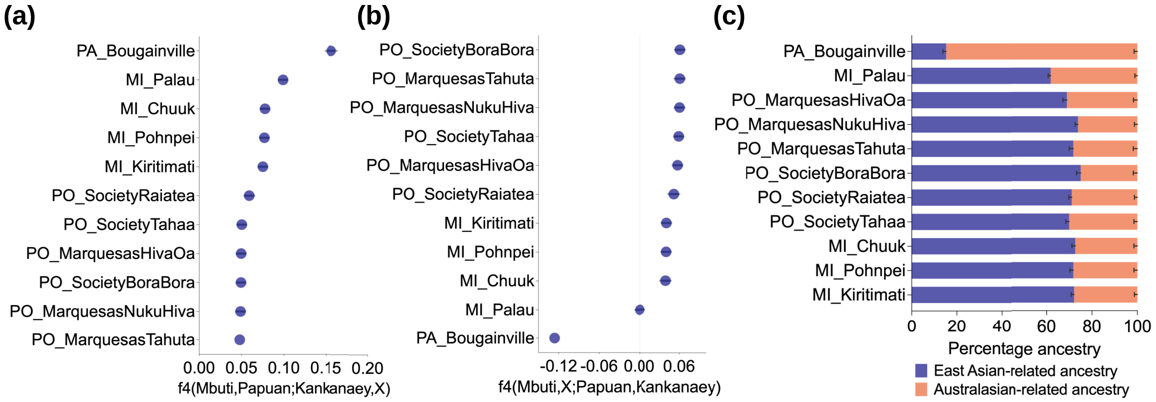

Fig. 5. East Asian and Australasian-related ancestries in Kiritimati. a) Detection of Australasian-related ancestry using the test f4(Mbuti, Papuan; Kankanaey, Kiritimati). Papuans represent the Australasian-related ancestry while Philippine Cordilleran Kankanaey represent the East Asian-related ancestry. b) Detection of higher levels of East Asian-related relative to Australasian-related ancestry in Kiritimati using the test f4(Mbuti, X; Papuan, Kankanaey). c) Proportions of East Asian-related and Australasian-related ancestries estimated by qpAdm in Kiritimati and other Micronesian and Polynesian populations. Error bars represent 1.96 standard error of the estimate. MI, Micronesian; PA, Papuan; PO, Polynesian; PH, Philippine.

groups in Island Southeast Asia, they share the highest number of IBD segments with non-Negrito populations from the Philippines.

Kiritimati Possess Some Papuan-Related Ancestry

To assess the presence of Australasian-related ancestry in Kiritimati, represented by Papuans, relative to the least admixed East Asian group, represented by the Philippine Cordilleran (Kankanaey), we employed the f4(Mbuti, Papuan; Kankanaey, Kiritimati) test. We find that Kiritimati has significant levels of Papuan-related ancestry ($Z > 3$), akin to those observed in other Micronesian and Polynesian groups (Fig. 5a).

We implemented the test f4(Mbuti, Kiritimati; X, Y), where X is a Papuan highlander group and Y a Cordiellran Kankanaey group, to determine whether Kiritimati has more Papuan-related or East Asian-related ancestry (Fig. 5b). In concordance with the Admixture analysis at $K = 3$, Kiritimati exhibits significantly higher levels of East Asian-related ancestry. When we then utilized qpAdm (Harney et al. 2021) to estimate the proportions of ancestries, Kiritimati's genetic make-up is ~28% Papuan-related and ~72% East Asian-related ancestries (Fig. 5c). Furthermore, we applied an LD-based method implemented in Malder (Loh et al. 2013) to determine the date of admixture between Papuan-related and East Asian-related ancestries, revealing this event to have occurred around 1,830 ± 390 years bp.

The influx of Papuan-related ancestry into Kiritimati has likely played a crucial role in shaping the population's genetic diversity, mitigating the impact of strong genetic drift often observed in isolated island populations. Genetic drift, resulting from recent bottlenecks or founder events, can lead to elevated levels of total runs of homozygosity (ROH) and inbreeding coefficients. Kiritimati, along with other Micronesian and Polynesian groups, exhibited relatively high mean levels of total ROH and inbreeding coefficients. However, these levels were still lower than those observed in other small isolated populations such as highlander Papuans, Mangyan Buhid of the Philippine island of Mindoro, and Karitiana of the Amazon rainforest in Brazil (Fig. 6a and b; supplementary fig. S2, Supplementary Material online). This suggests that the introduction of Papuan-related ancestry into Kiritimati has contributed to maintaining a more diverse genetic landscape, potentially preventing the extremes of genetic drift commonly seen in small isolated populations.

Limited West Eurasian Genetic Legacy Among Kiritimati

The presence of West Eurasian ancestry has been previously identified in certain Micronesian and Polynesian groups, reflecting the genetic imprint of European colonization in the region. To explore whether Kiritimati exhibits West Eurasian ancestry, we conducted the f4(Mbuti, European; X, Y) test. Consistent with historical records and prior research, we confirmed the existence of West Eurasian ancestry in Guam, Society, and Marquesas Island groups ($Z > 3$) (Hudjashov et al. 2018; Liu et al. 2022; Tätte et al. 2022).

In contrast, our analysis did not reveal significant levels of West Eurasian ancestry in Kiritimati. While Admixture analysis indicated that some Kiritimati individuals may display an ancestry component associated with West Eurasians, further scrutiny using the f4(Mbuti, French; X, Y) test, with X and Y representing various Kiritimati individuals, showed that only a single Kiritimati individual exhibited some degree of West Eurasian ancestry. Importantly, this observation was not statistically significant ($Z < 2.79$). Overall, these results suggest a relatively limited impact of recent West Eurasian gene flow into Kiritimati when compared to other populations in the surrounding area.

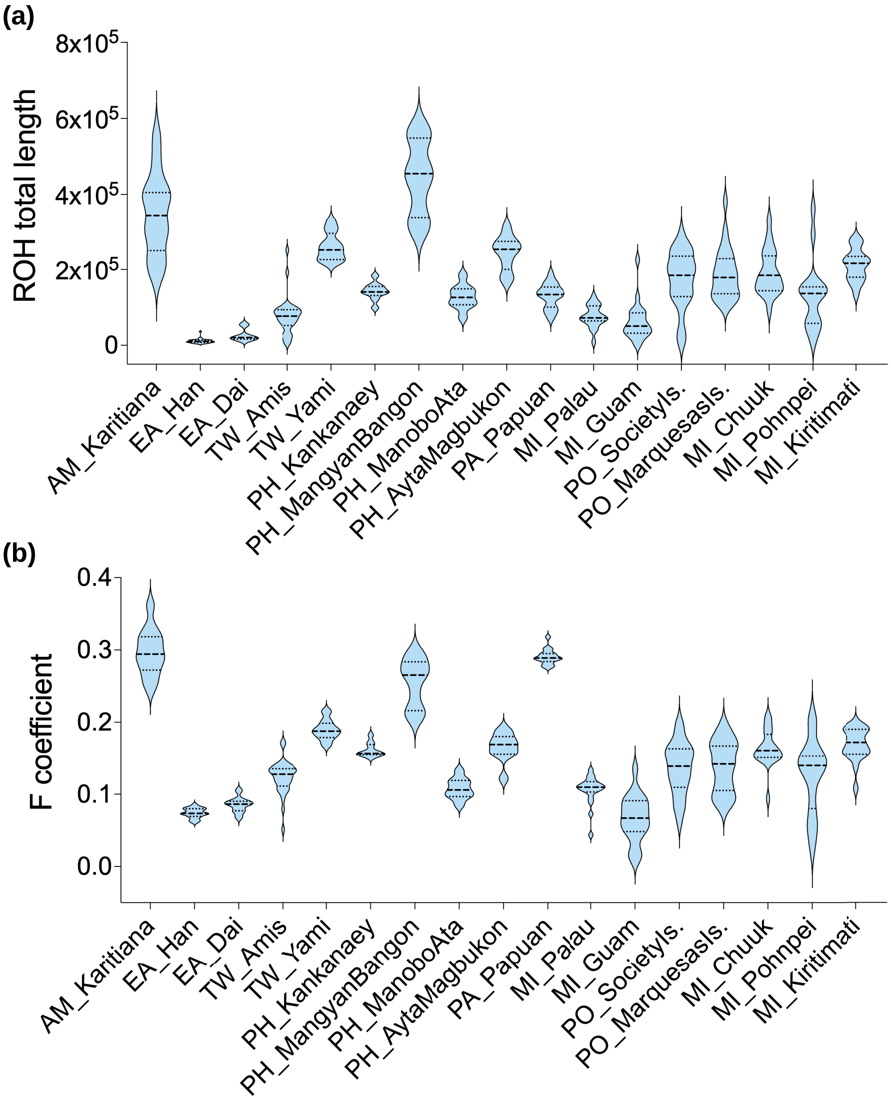

Fig. 6. Level of genetic differentiation in the Kiritimati. a) Runs of homozygosity and b) inbreeding coefficient of Kiritimati and other reference populations estimated using PLINK v1.9. AM, American; EA, East Asian; MI, Micronesian; PA, Papuan; PO, Polynesian; PH, Philippine; TW, Taiwanese.

Model of Kiritimati Population History

We utilized the qpGraph function of the Admixtools software package to test explicit models of the population history of Kiritimati. We started with simple population topologies with Mbuti as an outgroup, highlander Papuan as a surrogate for Papuan-related ancestry, and Taiwanese Amis and Philippine Kankanaey Cordilleran as surrogates for East Asian-related ancestry (supplementary fig. S3, Supplementary Material online). The model that is not rejected is when Kiritimati is an admixture between Papuan-related ancestry and an East-Asian-related ancestry that is associated more with Kankanaey than Amis (supplementary fig. S3c, Supplementary Material online).

We extended the model by adding other central-eastern Micronesians, and tested various configurations of genetic relationships between Kiritimati, Chuuk, and Pohnpei (supplementary fig. S4, Supplementary Material online). The model that fits best is when Kiritimati is an outgroup to the clade formed by Chuuk and Pohnpei. Additionally, we incorporated a Polynesian population into the model, Tahaa of Society Island (supplementary fig. S5, Supplementary Material online). The models that were not rejected are when Tahaa forms as an outgroup to central-eastern Micronesians, with additional gene flow from Kiritimati to Polynesians or from Polynesians to Kiritimati (supplementary fig. S5c and d, Supplementary Material online).

Archaeogenetic Analyses Links Kiritimati to Ancient Lapita

To complement our findings, we investigated the genetic affiliation of Kiritimati in relation to various ancient individuals in the region. Using the test f4(Mbuti, Kiritimati; Liangdao-2, X), where X represents any ancient Lapita or Micronesian individual, we discovered that Kiritimati shares more alleles with ancient Lapita or Micronesian populations relative to Liangdao-2, a 7,500-year-old ancient individual (supplementary fig. S6, Supplementary Material online). To further refine our analysis, we employed the test f4(Mbuti, Kiritimati; ancient Micronesia, ancient Lapita), determining that Kiritimati shows stronger genetic affiliation with 2,900-year-old Lapita Vanuatu or 2,500-year-old Lapita Tonga compared to any other ancient Micronesian groups from Guam or the Marianas Islands (supplementary fig. S6, Supplementary Material online). These genetic relationships, derived from a combination of f4 statistics, were supported by our admixture graph inference, which indicated that only models nesting Kiritimati from ancient Lapita, rather than ancient western Micronesian populations, were not rejected (supplementary fig. S7, Supplementary Material online).

Lastly, we utilized the test f4(Mbuti, Kiritimati; Lapita Vanuatu, Lapita Tonga) to directly assess whether Kiritimati has excess genetic sharing with one of the ancient Lapita individuals from Vanuatu or Tonga ($Z = 0.55$). Our results showed that Kiritimati is equidistant to both Lapita Vanuatu and Lapita Tonga. When constructing admixture graph models, the results did not distinguish whether Kiritimati is more closely related to Lapita Tonga or Lapita Vanuatu (supplementary fig. S8, Supplementary Material online). Collectively, these findings indicate that Kiritimati can trace its ancestral origins to the Lapita, specifically from an ancestral population of western Polynesians.

Discussion

The peopling of Oceania by Austronesian-speaking populations has long fascinated prehistorians. The islands of Kiribati are strategically located in a transitional region between Micronesia and Polynesia, which may serve as a vital migration pathway for various Austronesian-speaking groups. To advance our understanding of this critical juncture in human history, we investigated genome-wide data from the Kiritimati population of Kiribati, aiming to uncover their genetic roots and connections with other Oceanian populations.

Our findings reveal that the Kiritimati population predominantly exhibits Remote Oceanian-related East Asian ancestry (Figs. 1 to 6 and supplementary figs. S5 to S8, Supplementary Material online). This ancestry traces back to an ancestral group in the southern China-Taiwan region (Yang et al. 2020; Larena, Sanchez-Quinto et al. 2021; Wang et al. 2021), represented by 7,500-year-old Liangdao-2 individual (supplementary fig. S7, Supplementary Material online). A subset of this population migrated to the Philippines and subsequently into the Bismarck Archipelago 3,500 years ago, laying the foundations of the Lapita culture (Skoglund et al. 2016; Lipson et al. 2018; 2020; Posth et al. 2018; Choin et al. 2021). While studies often use Cordillerans from the Philippines as proxies for this ancestral group (Mörseburg et al. 2016; Larena, McKenna et al. 2021), our IBD analysis also identifies coastal southern Philippine populations like Mansaka and Sangil as similarly sharing the most IBD with Kiritimati (Fig. 4). This aligns with their maritime history, unlike the Cordillerans, who are primarily highland agriculturists (Larena, Sanchez-Quinto et al. 2021). This discrepancy is explained by the neighbor repulsion phenomenon in f statistics (Atağ et al. 2024), where a test population appears closer genetically to a distant population than to a neighboring source, due to external admixture obscuring the genetic signal. For instance, Sangil and Mansakan populations received gene flow from divergent groups containing Negrito-related, Papuan-related, and Manobo-related ancestries, while the Cordilleran groups remained relatively unadmixed.

Further corroborating previous studies (Liu et al. 2022; Palencia-Madrid et al. 2022), the East Asian component in Kiritimati and other central-eastern Micronesian populations, such as those from Chuuk and Pohnpei, originates from an ancestral Lapita population that settled in western Polynesia around 3,000 years BP (supplementary figs. S6 to S8, Supplementary Material online). This explains the strong genetic ties between Kiritimati, the ancient Lapita population of Tonga, and modern Polynesians, as evidenced by Admixture, PCA, f statistics, and IBD sharing analyses (Figs. 1 to 4 and 7 and supplementary figs. S1, S5 to S8, Supplementary Material online). Following the Lapita era, an ancestral Polynesian culture emerged in Tonga and Samoa (Anderson et al. 2000; Fischer 2002; Petersen 2009), leading to population dispersals into central and eastern Polynesia and likely into eastern Micronesia, contributing to the Polynesian-related ancestry seen today in Chuuk, Pohnpei, and the Gilbert Islands.

Following the settlement of the Gilbert Islands, there is anthropological evidence for continued interactions between Gilbertese and Samoans. For instance, Samoans introduced traditional meeting houses, known as "maneabas," and various socio-political structures to the Gilbert Islands (Talu et al. 1984; Fischer 2002; Petersen 2009). These interactions likely facilitated continuous gene flow between western Polynesians and eastern Micronesians, as evidenced by the excess allele sharing we observed between Kiritimati and Polynesians relative to central-eastern Micronesians (supplementary figs. S1 and S5, Supplementary Material online). Over the past century, waves of Gilbertese migration to Kiritimati occurred, initially involving coconut plantation workers, followed by nuclear test workers during the 1950s British-American testing programs, and more recently, postindependence migrations after 1979 (Petersen 2009; Thaman and Tye 2019).

It is also notable that the genetic data of the Kiritimati population aligns with linguistic evidence. The Gilbertese language, or Te taetae ni Kiribati, falls under the Micronesian branch of the Central-Eastern Oceanic languages, part of the larger Malayo-Polynesian family (Lynch 2002; Harald et al. 2024). This Central-Eastern Oceanic group also includes the Polynesian languages, such as Tongan from western Polynesia and Marquesan and Tahitian from eastern Polynesia. In contrast, western Micronesian languages, such as Palauan and Chamorro, belong to a different branch of the Malayo-Polynesian family, indicating a distinct origin from the languages of eastern Micronesia, like Gilbertese.

Papuan-related ancestry is present in all Kiritimati individuals (Figs. 2 and 5), with admixture dated to 1,440 to 2,220 years BP, younger than the East Asian-Papuan admixture date for Lapita individuals in Vanuatu (2,560 ± 477 years BP) (Posth et al. 2018). Interestingly, the oldest Lapita individuals from Tonga (2,320 to 2,690 years BP) (Skoglund et al. 2016), one of the ancient samples most closely related to Kiritimati, lack Papuan-related ancestry. This suggests that after the initial Lapita settlement, admixture with Papuan-related populations occurred first in Vanuatu and shortly thereafter in Tonga, aligning with the admixture dates detected in Kiritimati. Given that the admixture date predates the earliest archaeological evidence for human occupation of Kiritimati, which is between 1250 and 1450 CE (Anderson et al. 2000), this event likely occurred outside of Kiritimati. Thus, an admixed population in western Polynesia, such as ancestral Tongans and/or Samoans, likely represents the immediate genetic origins of the Kiritimati population.

Our analyses on ROH indicate a significant level of genetic drift in the Kiritimati population, higher than that observed in continental populations of East Asia such as Han and Dai. This is typical for a small island population in the Pacific undergoing a series of founder events. However, the genetic drift is not as extreme as that seen in the Karitiana of the Americas or the Mangyan Buhid of the Philippines, possibly due to past admixture with Papuan-related groups and recent continuous gene flow with other Polynesian populations (Palencia-Madrid et al. 2022).

The colonial history of the Gilbert Islands under British rule since the late 1800s, transitioning from a protectorate to a colony, has left a lasting cultural impact (Talu et al. 1984; Van Trease 1993; Macdonald 2001). Postindependence in 1979, English remains an official language, Christianity is predominant, and the governance structure is parliamentary. Despite these cultural influences, the genetic legacy of colonization is minimal, with only one individual out of 19 showing West Eurasian ancestry. This limited genetic impact is similar to other Southeast Asian populations, like those in the Philippines, Malaysia, and Indonesia. In contrast, Native Hawaiians (Kim et al. 2012), Chamorros of Guam (Liu et al. 2022), Rapa Nui of Easter Island (Fehren-Schmitz et al. 2017), and Maori of New Zealand (Friedlaender et al. 2008) exhibit a more pronounced genetic legacy of colonization, with West Eurasian ancestry present in a significant proportion of the population.

Altogether, our investigation highlights the intricate genetic history of the unique population of Kiritimati. Future studies involving ancient samples across various time periods in Island Southeast Asia and the Pacific will likely refine our understanding of the migration pathways and precise timings of the ancestral Kiritimati population.

Methods

Sampling and Ethical Considerations

Buccal swabs were collected from male Kiritimati individuals using Gentra Buccal Cell Kit (Puregene, Gentra Systems, Minneapolis, MN). All volunteer participants were at least 18 years old and all samples were collected from unrelated individuals (more than 2nd degree relationship). Participants were also asked to report on their parents' and grandparents' ethnicity, and only those who reported to have all 4 grandparents with Gilbertese ancestry were included in the study.

Sampling was performed in one fieldwork trip in 2016 in accordance with the ethical guidelines stipulated by Colorado College, Colorado Springs, Colorado USA, and under the supervision of the Department of Education of Kiritimati. Also, the study was implemented in accordance with the Declaration of Helsinki for the protection of human subjects and with the regulations of the UNESCO International Declaration on Human Genetic Data. All participants provided their informed consent before sampling, and was documented through a signed consent form. Fieldwork sampling and all experimental protocols were approved by the IRB of Colorado College (2014 08 29). In addition, the processing of samples and analysis of data was approved by the Regional Ethical Review Board in Uppsala, Sweden (Dnr 2021-05880-01). We maintained in contact with the representatives of the community, and provided them a layman summary of the findings in the form of a video and written summary of the findings. This material was provided to two community leaders who in turn distributed it to the school educators and administrators.

Sample Processing, Genotyping, and Data Processing

The buccal swab samples were processed for the QIAamp DNA Mini Kit (Qiagen, USA). Twenty purified DNA samples were sent to the SNP&SEQ Technology Platform at Uppsala Biomedical Center, Uppsala University for genotyping with Illumina Infinium assay (San Diego, CA) using the Infinium H3 Africa Consortium Array v2 (2,271,503 markers). The data generated were filtered for indels, duplicates, nonautosomal and unmapped single nucleotide polymorphism (SNP)s, and SNPs with 10% missingness. A single with more than 15% missing data was excluded, producing a Kiritimati base dataset with 19 individuals and 2,193,320 SNPs.

The base dataset was merged with a worldwide panel of populations from the Human Genome Diversity Project (Bergström et al. 2020) to produce a Panel 1 dataset with 1,402,707 SNPs. To cover more groups in Southeast Asia and Oceania, the Panel 1 dataset was merged with Illumina-based data from Taiwan (Tätte et al. 2021), Polynesia (Hudjashov et al. 2018; Tätte et al. 2022), and Micronesia to generate a Panel 2 dataset with 252,378 SNPs (Liu et al. 2022). Lastly, for comparative analysis with publicly available ancient DNA data, the Kiritimati base dataset was filtered for transversion sites, pseudohaploidized, and merged with v54_1240k Allen Ancient DNA Resource dataset (Skoglund et al. 2016; Yang et al. 2020; Liu et al. 2022; Mallick et al. 2024), to produce a Panel 3 dataset with 96,846 SNPs.

Population Genetic Analysis

Population structure was analyzed using ADMIXTURE v1.3 (Alexander, Novembre, and Lange 2009) and CLUMPP (Jakobsson and Rosenberg 2007), which was subsequently visualized using Pong v1.4 (Behr et al. 2016). We performed admixture proportion estimation in populations using qpAdmin, outgroup f3 statistics using qp3Pop, and formal tests of admixture using qpDstat of AdmixTools v5.0 package (Patterson et al. 2012). We utilized a weighted linkage disequilibrium (LD) statistic-based method, MALDER (Loh et al. 2013), to estimate dates of admixture. We computed measures of genetic diversity such as ROH and inbreeding coefficient using PLINK v1.9 (Purcell et al. 2007), and categorized the ROH into different tract lengths (Ceballos et al. 2018). Estimation of between population FST and PC analysis was performed using EIGENSOFT v7.1 (Patterson et al. 2006), and the estimation of pairwise f2 statistics was estimated using POPSTATS (Skoglund et al. 2015). Detection of shared identity-by-descent between populations was performed using Beagle 3.3.2 (Browning and Browning 2007). The analyses focused on the sharing of DNA segments between individuals from Kiritimati and the reference populations in our dataset. We extracted the number of shared segments between each pair of individuals from the results of the Refined IBD analysis (Browning and Browning 2013). Next, we calculated population medians for segments in the ranges of 0 to 1 cM, 1 to 2 cM, and greater than 2 cM to identify patterns of genetic sharing.

To construct admixture graphs and infer models of demographic history that best fit the data, we utilized the qpGraph tool of the ADMIXTOOLS v5.0 software package (Patterson et al. 2012). For a model with present-day populations, we used highlander Papuan as a surrogate for Australasian lineage, Kankanaey Cordilleran as a surrogate for Philippine non-Negrito lineage, and Amis as a surrogate for indigenous Taiwanese lineage. For a model with ancient DNA data, we used 7,500-year-old Liangdao-2 to represent source Austronesian-related lineage (Yang et al. 2020; Larena, Sanchez-Quinto et al. 2021); 2,900-year old Vanuatu and 2,500-year-old Tonga individuals as a surrogate for ancient Lapita (Skoglund et al. 2016); 2,800-year-old Guam Late Unai, 700-year-old Guam Latte, 600-year-old Guam Late Latte, and 600-year-old Marianas Island individuals as a surrogate for ancient Micronesians (Liu et al. 2022). Mbuti was used as an outgroup African population in all models, and Kiritimati was added to each model in various combinations to test the fit. We applied the following parameters in all analyses: outpop (NULL), diag (0.0001), hires (YES), blgsize (0.05), and lsqmode (YES), and utilized a worst fitting f statistical test of z-score >3 or any models with internal zero score drift branches as thresholds for model rejection.

Supplementary Material

Supplementary material is available at *Genome Biology and Evolution* online.

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Data Availability

The data generated in this study will be made available to researchers following a review and approval process by the Data Access Committee, which is overseen by the corresponding authors. The data have been deposited in the

European Genome-Phenome Archive under accession number EGAS00001008060.

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