Article

Stable Isotopic Evidence for Nutrient Rejuvenation and Long-Term Resilience on Tikopia Island (Southeast Solomon Islands)

Jillian A. Swift 1,*, Patrick V. Kirch 2, Jana Ilgner 3, Samantha Brown 4, Mary Lucas 3, Sara Marzo 3 and Patrick Roberts 3

Abstract: Tikopia Island, a small and relatively isolated Polynesian Outlier in the Southeast Solomon Islands, supports a remarkably dense human population with minimal external support. Examining long-term trends in human land use on Tikopia through archaeological datasets spanning nearly 3000 years presents an opportunity to investigate pathways to long-term sustainability in a tropical island setting. Here, we trace nutrient dynamics across Tikopia’s three pre-European contact phases (Kiki, Sinapupu, Tuakamali) via stable carbon and nitrogen isotope analysis of commensal Pacific rats (Rattus exulans) and domestic pig (Sus scrofa) bone and tooth dentine collagen. Our results show a decline in δ15N values from the Kiki (c. 800 BC–AD 100) to Sinapupu (c. AD 100–1200) phases, consistent with long-term commensal isotope trends observed on other Polynesian islands. However, increased δ15N coupled with lower δ13C values in the Tuakamali Phase (c. AD 1200–1800) point to a later nutrient rejuvenation, likely tied to dramatic transformations in agriculture and land use at the Sinapupu-Tuakamali transition. This study offers new, quantifiable evidence for deep-time land and resource management decisions on Tikopia and subsequent impacts on island nutrient status and long-term sustainability.

Keywords: stable isotopes; archaeology; commensals; nutrient flows; Polynesia; land use; ecomimicry

1. Introduction

The growing pressures of climate change, population increase, and disruptions to food supply networks highlight the ever-increasing need to establish food systems that are not only highly productive, but also sustainable and resilient in the long term. However, our means to evaluate sustainability across long time scales are limited. Archaeological collections preserve multiproxy ecological information, including faunal and botanical remains, soils, and ancient biomolecules that span centuries or even millennia. As such, these datasets afford a unique opportunity to investigate land use, ecosystem transformations, and impacts to agricultural systems across generations of human activity, e.g., [1–3]. Islands, especially those in Polynesia, have proven effective as ideal “model systems” for applying archaeological datasets to investigate human activities and environmental transformations on a global scale, e.g., [4–7].

‘Sustainability’ and ‘resilience’ are helpful concepts to galvanize research towards addressing contemporary environmental challenges. However, the utility of these concepts has been called into question due to their complex, multifaceted nature, often-nebulous definitions, and imprecise applications, e.g., [8–12]. A recent metaanalysis sought to find consensus in how these two terms were, respectively, defined and applied across a breadth...
of disciplinary literature [13]. Broadly, they concluded that the term sustainability was applied to ‘bottom-line’ management of social, environmental, and economic systems while resilience spoke to the long-term ability for a system to recover or to adapt in the face of disruption or persistent stress. We agree with these general distinctions, but also find it useful to generate situational definitions that can address specific facets of sustainability. Here, we define an archaeological agro-ecosystem as sustainable in the long term if there is no evidence for soil nutrient drawdown through time. By contrast, an agro-ecosystem meets the conditions of resiliency if it is either sustainable in the long term or if there is evidence for adaptation and recovery following earlier nutrient declines. Rather than a holistic determination of long-term sustainability, this study therefore seeks to characterize whether and how some facets of past agro-ecosystems were sustainable.

Previous work has established that stable isotope analysis of commensal animals can shed new light on transformations to past social and natural systems, e.g., [14–18]. This is in part due to commensal species’ unique position as animals that live in and around human settlements but whose diets are not actively managed by people. Rather than a strict biological definition of commensalism (an evolutionary species relationship wherein one benefits and the other experiences no impact), archaeologists tend to refer back to commensalism’s more literal translation of “sharing a table”. Commensals are therefore animals that scavenge from human meal scraps (or in other ways take advantage of human-modified environments) or, in the context of the “commensal pathway” to domestication, animals that fall somewhere between ‘wild’ and ‘domestic’ categorization (see [19]). In the Pacific, the term ‘commensal’ has been employed to describe the main animal species transported by Pacific peoples to new island environments: the pig (Sus scrofa), dog (Canis familiaris), chicken (Gallus gallus), and Pacific rat (Rattus exulans). However, in many cases, it is likely that pigs, dogs, and chickens were domesticated or at least their diets were to some extent managed by people [20–23].

In the present study, we employ commensal δ13C and especially δ15N values as a proxy for one facet of long-term sustainability and resilience in past agro-ecosystems: nutrient (predominantly nitrogen, N) availability. An important caveat is that δ15N values are not a direct measure of overall nitrogen abundance. Higher δ15N values do not necessarily correspond with higher overall nitrogen availability (and vice versa). However, changes in commensal δ15N can help characterize the processes influencing nitrogen flows across agro-ecosystems, and semi-quantitatively evaluate their degree of impact. While δ13C and δ15N are primarily employed for dietary reconstruction, changes to ‘baseline’ C and N stable isotope ratios in soils and primary producers are also carried up the food chain. Thus, influences on baseline δ13C and δ15N, such as climate change and growing conditions, e.g., [24–26], can also result in significant transformations to commensal δ13C and δ15N without any true change to commensal diet. This has been demonstrated in the Pacific, where human land use strategies and species extinction can be tied to significant changes in Pacific rat δ13C and δ15N [18,27].

Tikopia is often held up as a model for long-term sustainability in an isolated, circumscribed island environment [28–31]. The people of Tikopia have been able to maintain a remarkably dense population (c. 1200 people) for an island of its size (c. 4.6 km2) and relatively long chronology of permanent human settlement (c. 3000 years), with limited reliance on external resources. This sustainability is maintained through careful resource management strategies as well as rigorous population control mechanisms, such as family size limitations and emigration [32,33]. Of particular relevance is the system of intensive arboriculture or tree-cropping, what ethnographer Raymond Firth called “orchard gardening” [34]. This multistory arboricultural system mimicks the structure of the natural forests it replaces, but substitutes forest plants with similar species that provide food and other biocultural resources. Quintus et al. [35] have pointed to the importance of arboriculture or agro-forestry in traditional Polynesian subsistence systems (and see [36,37]).

Previous analysis of Tikopia’s archaeofauna showed initially high δ15N values in Pacific rat bone collagen, which sharply declined in later phases. This pattern fit within a
A small number of Kiki Ware sherds carry dentate-stamped designs that indicate connections to the Lapita pottery tradition. Similar early Lapita ceramics are found in the nearby Santa Cruz Islands and the southern end of Vanuatu [41,42], and initial Tikopian settlement is hypothesized to originate from the Bismarck or Solomon Islands to the west [38,40]. In the following Sinapupu Phase (c. AD 100–1200) local ceramic production ends, and Kiki Ware is replaced by non-local incised Mangaasi-style ceramics [43], likely imported from the Vanuatu archipelago to the south. In the final pre-contact Tuakamali Phase (c. AD 1200–1800), ceramic manufacture and use ends completely. This phase likely also marks the arrival of Polynesian peoples to Tikopia, which would be consistent with broader patterns of Polynesian migration and expansion across the Pacific (Kirch 2017). Oral traditions and new obsidian and volcanic glass sourcing data speak to fraught relationships between the Tikopia and invading Tongans during this time, perhaps as part of broader Tongan maritime polity expansion efforts [40,44]. Kirch and Yen [38] establish AD 1800 as an arbitrary date to mark the Historic Phase, as a transition between pre- and post-European contact.
Kirch and Yen [38] outlined a sequence of three pre-contact cultural phases for Tikopia: the Kiki, Sinapupu, and Tuakamali Phases. While new radiocarbon dates have updated their absolute chronology [39], the overall sequence and its defining characteristics have remained consistent. Time period boundaries are largely demarcated by changes in material culture: the earliest Kiki Phase (c. 800 BC to AD 100) is characterized by a diverse suite of *Tridacna* shell adzes, *Spondylus* shell bracelets, and most distinctively the locally made ‘Kiki Ware’ ceramics. A small number of Kiki Ware sherds carry dentate-stamped designs that indicate connections to the Lapita pottery tradition. Similar early Lapita ceramics are found in the nearby Santa Cruz Islands and the southern end of Vanuatu [41,42], and initial Tikopian settlement is hypothesized to originate from the Bismarck or Solomon Islands to the west [38,40]. In the following Sinapupu Phase (c. AD 100–1200) local ceramic production ends, and Kiki Ware is replaced by non-local incised Mangaasi-style ceramics [43], likely imported from the Vanuatu archipelago to the south. In the final pre-contact Tuakamali Phase (c. AD 1200–1800), ceramic manufacture and use ends completely. This phase likely also marks the arrival of Polynesian peoples to Tikopia, which would be consistent with broader patterns of Polynesian migration and expansion across the Pacific (Kirch 2017). Oral traditions and new obsidian and volcanic glass sourcing data speak to fraught relationships between the Tikopia and invading Tongans during this time, perhaps as part of broader Tongan maritime polity expansion efforts [40,44].

In addition to these changes in material culture, Kirch and Yen [38] identified several significant transformations to the island’s topography, environment, and patterns of human land use over time. However, these changes are not sharply demarcated across archaeological phases (Summary in Table 1). They estimate that during the Kiki Phase, the island’s land area was only around 72% of its current size, while conversely the reef flats were around 70% larger [38:325]. This reflects geomorphic changes associated with a +1 m mid-Holocene sea level stand. Land area apparently remained consistent across the Kiki and Sinapupu phases; however, continued forest clearance and erosion gradually displaced sediment from the volcanic hillsides into an increasingly aggraded shoreline. By contrast, significant transformations occurred throughout the Tuakamali Phase. Shorelines expanded, which created new landmass, reduced the size of reef flats, and generated new swampland environments that had not existed previously. Very late in the Tuakamali Phase (sometime after first European contact in AD 1606, according to their accounts), the formation of a sandy tombolo (the Ravenga area) and its eventual enclosure transformed what was previously a saltwater bay into a brackish lake known as Te Roto.

**Figure 1.** Map of Tikopia (Southeast Solomon Islands), with site source locations for archaeofaunal assemblages labeled: TK-4, TK-20, and the Sinapupu Deposits (TK-1, TK-35, TK-36, and Transect).
Table 1. Key aspects of Tikopian environment and human land use roughly separated by archaeological phase.

| Phase                  | Key Aspects                                                                 |
|------------------------|-----------------------------------------------------------------------------|
| Kiki Phase (c. 800 BC to AD 100) | Introduction of new cultivars and commensal pig, dog, rat; extinctions/extirpations of avifaunal species; reliance on marine resources and large-bodied prey; fire use for forest clearance and agriculture; small-scale slash-and-burn agricultural activities |
| Sinapupu Phase (c. AD 100 to 1200) | Settlement expansion; expanded forest clearance; shoreline aggradation; colluvial deposition of nutrient-rich agricultural soils into the lowlands; continuing slash-and-burn agriculture; development of multistory arboriculture |
| Tuakamali Phase (c. AD 1200 to 1800) | Cessation of fire use for forest clearance or agriculture; shoreline expansion; reduction in the reef flats; closure of Ravenga tombolo and creation of brackish lake Te Roto; continued intensification of pig husbandry followed by a sudden, late extirpation of pig; complete establishment of multistory arboricultural system |

Kirch and Yen [38] found limited direct paleobotanical evidence for early cultivation, however it is likely that even the earliest inhabitants of Tikopia were skilled horticulturalists of traditional Pacific crops such as yams, taro, and breadfruit. Early forest clearance also created new opportunities for agricultural expansion. Sediment redistribution from the upper volcanic slopes generated new fans of nutrient-rich colluvial sediment; this was perhaps a deliberate strategy to increase the availability of agriculturally viable soils in the lowlands. Analysis of charcoal from these colluvial fans (particularly from excavations in the Rakisu agricultural zone) also suggest that Tikopians continued to employ fire in swidden agricultural activities for many centuries after initial clearance. The eventual disappearance of charcoal from these deposits indicates an eventual cessation of fire use for agriculture. Sediment deposition into the Rakisu zone also slowed, pointing to a gradual transformation in agricultural activities across the late Sinapupu and Tuakamali Phases into the multistory forest system present today [38].

Faunal assemblages offer tangible evidence for other aspects of food production and procurement activities across these phases. Early Kiki faunal assemblages are characteristic of assemblages from other early human occupation sites in the Pacific, and include abundant and diverse avifaunal remains, many of which are only found in the Kiki Phase; large quantities of turtle bone; larger-sized mollusks; and the human-introduced pig (Sus scrofa), dog (Canis familiaris), and Pacific rat (Rattus exulans). In the Sinapupu Phase (c. 100 BC to AD 1200), agricultural products alongside a mix of terrestrial and marine animal resources constituted the majority of Tikopian diet. However, the formerly abundant quantities of wild fauna diminished in favor of expanded terrestrial agricultural activities and intensified husbandry of domestic pigs. Turtle remains disappeared from the faunal record entirely, and the formerly abundant remains of birds, fish, and shellfish were supplemented by increasing quantities of pig bone. The reduced abundance and diversity of avifaunal remains in the Sinapupu Phase indicate extinctions, extirpations, and reductions in avifaunal populations. Despite the long-term decline in available reef habitat, marine resources remained an important contribution to Tikopian subsistence throughout its history. However, pig husbandry also intensified throughout the Tuakamali Phase, with pig becoming a major aspect of the terrestrial production system. At some point during the late Tuakamali Phase, pigs were apparently extirpated; pig faunal remains disappear entirely from archaeological deposits and ethnographically, pig populations were not maintained on Tikopia [38].

Most of the food production strategies in place by the Tuakamali Phase continue to be practiced by the Tikopia [31,34]. Agricultural practices remain oriented around multistory arboriculture and extend across the entire island, with nearly all available land either under cultivation or fallow. Aquatic resources from the surrounding reef, brackish lake, and (less frequently) open ocean are the dominant protein source. Although pigs were extirpated in the late Tuakamali Phase, a small number of pigs and chickens have been
reintroduced to Tikopia. In 2010, Mertz et al. estimated approximately 1000 chickens (an average of 9.5 per household) and 13 pigs were likely to inhabit the island [31]. Outside foods arrive infrequently and irregularly enough that they are not relied on, though food shortages on Tikopia have necessitated outside food relief—along with other crucial supplies—usually after severe cyclone events [45]. While contemporary reports offer fine-grained understanding of current sustainability mechanisms on Tikopia, this study applies commensal stable isotope analysis to understand their development and contributions to Tikopia’s long-term sustainability and resiliency.

2. Materials and Methods

2.1. Sample Selection

This study combines novel rat and pig samples with previously published Pacific rat stable isotope data [18] selected from the same Tikopia archaeological collections (Table 2). These collections were excavated by Kirch and Yen in 1977–78 and are now housed at the Bernice Pauahi Bishop Museum in Honolulu, HI. All samples were analyzed with permission from the museum through a destructive analysis loan. Pacific rat bone elements were selected by calculating the minimum number of individuals (MNI) within each site, unit, and layer in order to reduce the risk of resampling from the same individual while maximizing sample sizes. Femora were selected whenever possible for consistency. Femora are relatively large and robust, and therefore tend to preserve in the archaeological record more frequently and offer larger sample sizes. Elements were compared between levels for potential matching pairs to further control for double sampling. Similar procedures were followed for pig remains. However, deposition and preservation processes are considerably different for pig remains compared to rats. Pig teeth were selected wherever possible, as these were generally the most well preserved and readily identifiable elements.

Table 2. All new pig and rat bone elements selected for analysis and their archaeological contexts as recorded on collection bag labels.

| Sample No. | Site | Unit | Depth | Species | Element                  | Side |
|------------|------|------|-------|---------|--------------------------|------|
| TKSUS-1    | TK-36| C2   | Layer I | Sus scrofa | Upper Incisor | nd   |
| TKSUS-2    | TK-36| C4   | Layer I | Sus scrofa | Upper Molar 2 | nd   |
| TKSUS-3    | TK-36| C2   | Layer III | Sus scrofa | Lower Incisor | nd   |
| TKSUS-4    | TK-1 | J7   | Level 1 (0–20 cmbs) | Sus scrofa | Lower Premolar 3 | nd   |
| TKSUS-5    | TK-1 | J5   | 110–155 cmbs | Sus scrofa | Lower Molar 3 | nd   |
| TKSUS-6    | TK-1 | J8   | 125–160 cmbs | Sus scrofa | Lower Premolar 3 | nd   |
| TKSUS-7    | TK-1 | J9   | 140–160 cmbs | Sus scrofa | Lower Premolar 2 | nd   |
| TKSUS-8    | TK-1 | J10  | 140–200 cmbs | Sus scrofa | Upper Premolar 4 | nd   |
| TKSUS-9    | TK-1 | J5   | Level 2 (20–40 cmbs) | Sus scrofa | Lower Incisor | nd   |
| TKSUS-10   | TK-1 | J7   | 55–75 cmbs | Sus scrofa | Lower Incisor | nd   |
| TKSUS-11   | TK-1 | J7   | 85–140 cmbs | Sus scrofa | Upper Incisor | nd   |
| TKSUS-12   | TK-1 | J5   | Layer II (40–55 cmbs) | Sus scrofa | Deciduous Lower Premolar 4 | nd   |
| TKSUS-13   | TK-1 | J9   | Layer I | Sus scrofa | Lower Premolar 2 | nd   |
| KKSUS-14 **| TK-1 | J10  | Layer I | Sus scrofa | Deciduous Upper Incisor | nd   |
| TKSUS-15   | TK-36| B3   | Layer I | Sus scrofa | Upper Incisor | nd   |
| TKSUS-16   | TK-36| B3   | Layer I | Sus scrofa | Upper Premolar 4 | nd   |
| TKSUS-17   | TK-36| C1   | Layer I | Sus scrofa | Lower Incisor | nd   |
| TKSUS-18   | TK-36| B4   | Layer I (Upper) | Sus scrofa | Deciduous Upper Molar 1 | nd   |
| TKSUS-19   | TK-36| B4   | Layer I (Upper) | Sus scrofa | Lower Incisor | nd   |
| TKSUS-20   | TK-36| B2   | Layer III | Sus scrofa | Deciduous Lower Premolar 2 | nd   |
| TKSUS-21   | TK-20| J15  | 0–40 cm | Sus scrofa | Undetermined Molar Fragments | nd   |
| TKSUS-22   | TK-20| J13  | 35-Base | Sus scrofa | Upper Premolar 4 | nd   |
| TKSUS-23   | TK-20| J14  | 25-Base | Sus scrofa | Lower Premolar 3 | nd   |
| Sample No.  | Site | Unit                | Depth          | Species       | Element          | Side |
|------------|------|---------------------|----------------|---------------|------------------|------|
| TKSUS-24   | TK-20| J14                 | 0–25 cm        | *Sus scrofa*  | Upper Incisor    | nd   |
| TKSUS-25   | TK-35| C3                  | Level 1/Layer I| *Sus scrofa*  | Upper Premolar 4  | nd   |
| TKSUS-26   | TK-35| C3                  | Level 1/Layer I| *Sus scrofa*  | Upper Molar 1    | nd   |
| TKSUS-27   | TK-35| C3                  | Level 1/Layer I| *Sus scrofa*  | Upper Molar 1    | nd   |
| TKSUS-28a  | TK-35| B3                  | Level 1/Layer I| *Sus scrofa*  | Upper Molar 1    | nd   |
| TKSUS-28b  | TK-35| B3                  | Level 1/Layer I| *Sus scrofa*  | Upper Molar 2    | nd   |
| TKSUS-29   | TK-35| C1                  | Level 1/Layer I| *Sus scrofa*  | Upper Premolar 4  | nd   |
| TKSUS-30   | TK-35| C2                  | Level 1/Layer I| *Sus scrofa*  | Lower Molar 1    | nd   |
| TKSUS-31   | TK-35| C3                  | Level 3        | *Sus scrofa*  | Lower Incisor    | nd   |
| TKSUS-32   | TK-35| B3                  | Level 3        | *Sus scrofa*  | Upper Molar 1    | nd   |
| TKSUS-33   | TK-35| C2                  | Level 3        | *Sus scrofa*  | Deciduous Upper Premolar 3 | nd |
| TKSUS-34   | TK-35| C1                  | Level 3        | *Sus scrofa*  | Upper Premolar 3  | nd   |
| TKSUS-35   | TK-35| C1                  | Level 3        | *Sus scrofa*  | Lower Molar 1    | nd   |
| TKSUS-36   | TK-35| C2                  | Level 3        | *Sus scrofa*  | Lower Molar 3    | nd   |
| TKSUS-37   | TK-35| C2                  | Level 3        | *Sus scrofa*  | Lower Incisor    | nd   |
| TKSUS-38   | TK-35| C1                  | Level 4        | *Sus scrofa*  | Lower Molar 2    | nd   |
| TKSUS-39   | TK-35| C1                  | Level 4        | *Sus scrofa*  | Lower Incisor    | nd   |
| TKSUS-40   | TK-36| A2                  | Layer I        | *Sus scrofa*  | Lower Incisor    | nd   |
| TKSUS-41   | TK-36| A4                  | Layer (Lower)  | *Sus scrofa*  | Upper Incisor    | nd   |
| TKSUS-42   | TK-36| A4                  | Layer (Lower)  | *Sus scrofa*  | Lower Incisor    | nd   |
| TKSUS-43   | TK-36| A4                  | Layer (Upper)  | *Sus scrofa*  | Lower Incisor    | nd   |
| TKSUS-44   | Transect TP-47| Layer I | *Sus scrofa*  | Upper Premolar 4  | nd   |
| TKSUS-45   | Transect TP-47| Layer I | *Sus scrofa*  | Deciduous Lower Premolar 4 | nd |
| TKSUS-46   | Transect TP-48| Layer I | *Sus scrofa*  | Upper Molar 2  | nd   |
| TKSUS-47   | Transect TP-49| Layer I | *Sus scrofa*  | Lower Premolar 4 | nd |
| TKSUS-48   | Transect TP-50| Layer I | *Sus scrofa*  | Upper Molar 2  | nd   |
| TKSUS-49   | Transect TP-51| Layer I | *Sus scrofa*  | Upper Molar 1  | nd   |
| TKSUS-50   | Transect TP-51| Layer II | *Sus scrofa*  | Deciduous Lower Canine | nd |
| TKSUS-51   | Transect TP-47| Layer III| *Sus scrofa*  | Upper Molar 1 | nd   |
| TKSUS-52   | Transect TP-46| Layer IV | *Sus scrofa*  | Lower Molar 2  | nd   |
| TKSUS-53   | TK-35| A1                  | Level 1/Layer I| *Sus scrofa*  | Upper Molar 2    | nd   |
| TKSUS-54   | TK-35| A2                  | Level 1/Layer I| *Sus scrofa*  | Deciduous Upper Premolar 4 | nd |
| TKSUS-55   | TK-35| A2                  | Level 1/Layer I| *Sus scrofa*  | Upper Molar 3    | nd   |
| TKSUS-56   | TK-35| A2                  | Level 1/Layer I| *Sus scrofa*  | Deciduous Upper Premolar 4 | nd |
| TKSUS-57   | TK-35| A2                  | Level 1/Layer I| *Sus scrofa*  | Lower Molar 1    | nd   |
| TKSUS-58   | TK-35| A3                  | Level 1/Layer I| *Sus scrofa*  | Upper Molar 2    | nd   |
| TKSUS-59   | TK-35| A3                  | Level 1/Layer I| *Sus scrofa*  | Upper Molar 1    | nd   |
| TKSUS-60   | TK-35| B1                  | Level 1/Layer I| *Sus scrofa*  | Lower Molar 2    | nd   |
| TKSUS-61   | TK-35| A2                  | Level 2        | *Sus scrofa*  | Deciduous Lower Premolar 2 | nd |
| TKSUS-62   | TK-35| A3                  | Level 2        | *Sus scrofa*  | Lower Incisor    | nd   |
| TKSUS-63   | TK-35| A3                  | Level 3        | *Sus scrofa*  | Upper Incisor    | nd   |
| TKSUS-64   | TK-35| A3                  | Level 3        | *Sus scrofa*  | Upper Incisor 1  | nd   |
| TKSUS-65   | TK-35| B2                  | Level 1/Layer I| *Sus scrofa*  | Deciduous Lower Premolar 4 | nd |
| TKSUS-66   | TK-35| B1                  | Level 3        | *Sus scrofa*  | Lower Premolar 3  | nd   |
| TKSUS-67   | TK-35| B1                  | Level 3 (120–150 cms) | *Sus scrofa* | Upper Incisor | nd   |
| TKSUS-68   | TK-35| B2                  | Level 4        | *Sus scrofa*  | Upper Premolar 4  | nd   |
| TKSUS-69   | TK-35| B1                  | Level 3 (100–120 bs) | *Sus scrofa* | Lower Molar 1 | nd   |
| TKSUS-70   | TK-35| B2                  | Level 3 (above stones) | *Sus scrofa* | Lower Premolar 3 | nd   |
| TKSUS-71   | TK-35| B3                  | Level 5        | *Sus scrofa*  | Upper Premolar 4  | nd   |
| TKSUS-72   | TK-35| B3                  | Level 5        | *Sus scrofa*  | Lower Premolar 2  | nd   |
| TKSUS-73   | TK-35| C1                  | Level 4        | *Sus scrofa*  | Deciduous Upper Premolar 3 | nd |
| TKR-69     | TK-35| C2                  | Layer I        | *Rattus exulans* | Femur | L |
| TKR-70     | TK-35| C2                  | Layer I        | *Rattus exulans* | Femur | L |
| TKR-71     | TK-35| A2                  | Level 2        | *Rattus exulans* | Femur | L |
| TKR-72     | TK-35| A2                  | Level 2        | *Rattus exulans* | Femur | L |
| TKR-73     | TK-35| A2                  | Level 3        | *Rattus exulans* | Femur | L |
| TKR-74     | TK-35| A2                  | Level 3        | *Rattus exulans* | Femur | L |
Table 2. Cont.

| Sample No. | Site  | Unit | Depth  | Species          | Element | Side |
|------------|-------|------|--------|------------------|---------|------|
| TKR-75     | TK-35 | C1   | Level 4| *Rattus exulans* | Femur   | L    |
| TKR-76     | TK-35 | C1   | Level 4| *Rattus exulans* | Femur   | L    |
| TKR-77     | TK-35 | C3   | Level 3| *Rattus exulans* | Tibia   | R    |
| TKR-79     | TK-35 | A1   | Level 3| *Rattus exulans* | Femur   | L    |
| TKR-80     | TK-35 | C2   | Level 2| *Rattus exulans* | Femur   | L    |
| TKR-81     | TK-35 | A3   | Level 2| *Rattus exulans* | Tibia   | R    |
| TKR-82     | TK-35 | A1   | Level 2| *Rattus exulans* | Femur   | R    |
| TKR-83     | TK-35 | B3   | Level 2| *Rattus exulans* | Femur   | L    |
| TKR-84     | TK-35 | A2   | Layer I| *Rattus exulans* | Femur   | L    |
| TKR-85     | TK-35 | B3   | Layer I| *Rattus exulans* | Tibia   | R    |
| TKR-86     | TK-35 | C3   | Layer I| *Rattus exulans* | Humerus | R    |
| TKR-87     | TK-36 | C4   | Layer I| *Rattus exulans* | Femur   | L    |
| TKR-88     | TK-20 | T20  | No depth recorded| *Rattus exulans* | Humerus | R    |
| TKR-89     | TK-20 | J13  | 0–35 cm| *Rattus exulans* | Femur   | R    |
| TKR-90     | TK-20 | J14  | 25-base| *Rattus exulans* | Femur   | R    |
| TKSUS-74   | TK-36 | A3   | Layer III (lower)| *Sus scrofa* | Proximal phalanx | R |
| TKSUS-75   | TK-36 | C3   | Layer III| *Sus scrofa* | Metapodial | nd  |
| TKSUS-76   | TK-36 | C2   | Layer III| *Sus scrofa* | Proximal phalanx | R |
| TKSUS-77   | TK-35 | B3   | Level 5 | *Sus scrofa* | Ischium fragment | R |
| TKSUS-78   | TK-35 | B3   | Layer III| *Sus scrofa* | Aastragalus | L |
| TKSUS-79   | TK-35 | C3   | Level 4 | *Sus scrofa* | Calcaneum | L |
| TKSUS-80   | TK-35 | C2   | Level 5 | *Sus scrofa* | Aastragalus | L |
| TKSUS-81   | TK-35 | C2   | Level 4 | *Sus scrofa* | Mandible fragment | R |
| TKSUS-82   | TK-35 | C2   | Level 3 | *Sus scrofa* | Ulna | R |

* Species identification confirmed via ZooMS. ** Sample later eliminated from analysis due to dubious contextual information. nd = side not determined.

The faunal specimens used in this analysis were initially identified as either Pacific rat (*Rattus exulans*) or pig (*Sus scrofa*) by former Bishop Museum zoologist Alan Ziegler, and confirmed by Swift using comparative skeletons of Pacific rat, brown rat (*Rattus norvegicus*), black rat (*Rattus rattus*), and pig available through the Anthropology Department at Bishop Museum and the Museum of Vertebrate Zoology at the University of California, Berkeley. The large spiny rat (*Rattus praetor*) is the only other rodent known from pre-contact Tikopian faunal assemblages, and it appears as early as the late Kiki Phase. Few *R. praetor* elements were recovered from excavations and due to their rarity were not included in our analysis, though this is an intriguing avenue for future research. The large size and robustness of spiny rat bone elements generally render them distinguishable from Pacific rat, however the visual taxonomic identification of four of the largest Pacific rat femora was also confirmed through collagen peptide mass fingerprinting (ZooMS), conducted at the Max Planck Institute for the Science of Human History in Jena, Germany.

2.2. Taxonomic Identification via Zooarchaeology by Mass Spectrometry (ZooMS)

Four of the largest rat femora identified as likely to be Pacific rat (*Rattus exulans*) were also analyzed via collagen peptide mass fingerprinting to reconfirm species identification. Analysis was carried out following previously published protocols [46,47]. Briefly, the femora were submerged in 100 µL of 50 mM ammonium bicarbonate (AmBic) and allowed to soak overnight. The AmBic was then replaced and the femora were incubated at 65 °C for one hour. The supernatant was then removed from the femora which were allowed to dry. Then, 50 µL of the supernatant was frozen at −20 °C and stored as a backup. The remaining 50 µL was treated with 0.1 µg trypsin (Pierce™ Trypsin Protease, Thermo Scientific) and incubated at 37 °C for 18 h. Following collagen extraction and digestion, the samples were subjected to C18 clean-up with a matrix solution of α-cyano-4-hydroxycinnamic of 10 mg/mL in 50% ACN/0.1% TFA and allowed to co-crystallize.
All samples were spotted onto a ground steel plate in duplicate and analyzed using a Bruker Autoflex Speed LRF MALDI ToF mass spectrometer. The resulting mass spectra were peak picked with a signal to noise ratio of 3.5 using mMass (83) after baseline correction, smoothing, and deisotoping with the default parameters. The spectra were then compared to a reference library of known peptide markers for identification [48–52].

2.3. Carbon and Nitrogen Stable Isotope Analysis of Bone and Tooth Dentine Collagen

Stable carbon and nitrogen isotope analysis have long been applied in archaeology to reconstruct the diets of past humans and animals through analysis of (generally bone) tissue [53,54]. Differences in carbon fractionation between C\textsubscript{3}, C\textsubscript{4}, and CAM photosynthetic pathways result in distinct values for each plant group [55,56]. These differences are passed along to consumers, such that animals have δ\textsuperscript{13}C values which resemble the values of plants consumed at the base of their food chain. In Pacific contexts, most food crops are C\textsubscript{3} plants (−35 to −21‰), including taro (Colocasia esculenta), yams (Dioscorea sp.), sweet potato (Ipomoea batatas), and breadfruit (Artocarpus altilis). C\textsubscript{4} plants (−15 to −11‰) include sugarcane (Saccharum officinarum), seagrapes (Coccoloba uvifera) and many varieties of tropical grasses. Marine primary producers take in carbon from a mixture of sources, predominantly seawater bicarbonate, causing δ\textsuperscript{13}C values of marine food sources to most closely resemble those of C\textsubscript{4} plants [57].

Stable nitrogen isotope ratios are primarily useful for evaluating trophic position and marine versus terrestrial resource use. A stepwise δ\textsuperscript{15}N increase of roughly 3–5‰ accompanies every step up the consumer chain [58–60]. Additionally, because marine food webs tend to be longer and more complex than terrestrial systems, a given marine consumer will generally exhibit higher δ\textsuperscript{15}N values than their terrestrial counterparts. Secondarily, δ\textsuperscript{15}N values are also impacted by a range of nondietary factors including physiological, climatic, and environmental variability, e.g., [24,61,62]. Rat δ\textsuperscript{15}N values in the Pacific have shown to be especially sensitive to baseline δ\textsuperscript{15}N changes brought about by modifications of soil and nitrogen sources, e.g., [25,63]. Notably, reductions in δ\textsuperscript{15}N-rich seabird guano inputs, brought about by avifaunal extinctions and extirpations, have been linked to declines in rat δ\textsuperscript{15}N values on multiple Polynesian islands [18].

The pig and rat samples utilized in this study were prepared and analyzed at the Max Planck Institute for the Science of Human History (MPI-SHH) in Jena, Germany. Samples were prepared following the modified Longin method described in Richards and Hedges [64]. Samples were soaked in 0.5 M HCl until demineralized to collagen ‘pseudomorphs.’ Samples were rinsed then heated for 48 h at 70 °C in water acidified to pH 3, then removed from heat and immediately filtered through EZee Filter separators. Finally, samples were freeze dried and weighed into tin caps for analysis. When sample size allowed, samples were analyzed in duplicate and results reflect their mean values. Mass spectrometry analysis for all new samples was conducted at the MPI-SHH Stable Isotope Laboratory via ConFlo IV Thermo Scientific Isotope Mass Ratio Spectrometer (IRMS) coupled with a Thermo Scientific FLASH 2000 HT Elemental Analyzer (Thermo, Bremen, Germany).

Isotopic values are reported as the ratio of the heavier isotope to the lighter isotope (\textsuperscript{13}C/\textsuperscript{12}C or \textsuperscript{15}N/\textsuperscript{14}N) as δ values in parts per mille (‰) relative to international standards, VPDB for δ\textsuperscript{13}C and atmospheric N2 (AIR) for δ\textsuperscript{15}N. Results were calibrated against international standards of (IAEA-N-2 Ammonium Sulfate: δ\textsuperscript{15}N = +20.3 ± 0.2‰, USGS40 L-Glutamic Acid: δ\textsuperscript{13}C = −26.389 ± 0.042 ‰, δ\textsuperscript{15}N = −4.5 ± 0.1‰, IAEA-CH-6 Sucrose: δ\textsuperscript{13}C = −10.449 ± 0.03‰) and a laboratory standard (fish gelatine). Based on replicate analyses of standards machine measurement error is c. ±0.1‰ for δ\textsuperscript{13}C and ±0.1‰ for δ\textsuperscript{15}N. Overall measurement precision was studied through the measurement of repeat extracts from a fish enamel standard (n = 20, ±0.1‰ for δ\textsuperscript{13}C and ±0.1‰ for δ\textsuperscript{15}N).
3. Results

ZooMS analysis confirmed that each of the four analysed femora bore collagen peptides which matched published reference markers for *Rattus exulans* (Table 3). The high quality of the spectra obtained means this identification can be made to the exclusion of all other published Muridae.

Table 3. Collagen peptide markers from four Tikopia *Rattus* sp. specimens of especially large size. Full data available through Zenodo [65].

| Sample # | ID       | COL1α1 506–519 | COL1α2 976–990 | COL1α2 484–498 | COL1α2 502–519 | COL1α2 220–237 | COL1α2 793–816 | COL1α2 454–483 | COL1α1 586–618 | COL1α1 757–789 | COL1α2 757–789 |
|----------|----------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| TK2-13   | *Rattus* | 1105.7         | 1187.7         | 1203.7/1203.8  | 1453.9         | 1593           | 1586.9         | 2143.3         | 2883.7         | 2899.7         | 2957.7         |
| TK2-15   | *Rattus* | 1105.7         | 1187.7         | 1203.7/1203.8  | 1453.9         | 1593           | 1586.9         | 2143.4         | 2883.7         | 2899.7         | 3004.7         |
| TK2-16   | *Rattus* | 1105.6         | 1187.7         | 1203.7/1203.8  | 1453.9         | 1593/1566.9    | 1586.9         | 2143.3         | 2883.6         | 2899.6         | 3004.7         |
| TK2-20   | *Rattus* | 1105.6         | 1187.7         | 1203.7/1203.8  | 1453.9         | 1593/1566.9    | 1586.9         | 2143.3         | 2696.5         | 2883.6         | 2899.6         |

Table S1 (in Supplementary Material) presents bone collagen δ¹³C and δ¹⁵N results with quality control indicators for all new and previously published specimens. Graphs and statistical analyses were produced with R version 4.0.3 [66] using the dplyr package for data manipulation [67] and ggplot2 package for data visualization [68]. Data normality was evaluated using a Shapiro–Wilk’s test, and found to exhibit normal (p > 0.05, δ¹⁵Npig, δ¹⁵Ncommensal) and non-normal (p < 0.05, δ¹³Cpig, δ¹³Crat, δ¹⁵Nrat δ¹³C(commensal)) distributions. Given this variability, statistically significant differences in δ¹³C and δ¹⁵N values across archaeological phases were evaluated using a Kruskal–Wallis Test followed by a post hoc Pairwise Mann–Whitney–Wilcoxon Test when p < 0.05. Descriptive statistics and results of significance tests are reported in Table 4, Tables S2 and S3 (in Supplementary material).

Table 4. Summary statistics for commensal bone collagen δ¹³C and δ¹⁵N by phase.

| Phase | n   | Mean δ¹³C (‰) | SD δ¹³C (‰) | Min δ¹³C (‰) | Max δ¹³C (‰) | Mean δ¹⁵N (‰) | SD δ¹⁵N (‰) | Min δ¹⁵N (‰) | Max δ¹⁵N (‰) |
|-------|-----|----------------|-------------|--------------|-------------|----------------|-------------|--------------|-------------|
| Rat (*Rattus exulans*) |
| Kiki  | 23  | −17.4          | 1.9         | −20.4        | −14.1       | 13.2           | 1.3         | 11.3         | 16.1        |
| Sinapupu | 8    | −19.7          | 0.7         | −21.0        | −18.6       | 9.4            | 1.2         | 7.6          | 10.9        |
| Tuakamali | 13   | −19           | 1.7         | −23.0        | −17.0       | 11.4           | 1.8         | 8.7          | 15.0        |

| Pig (*Sus scrofa*) |
| Kiki  | 6   | −19.3          | 1           | −20.7        | −18.3       | 9.7            | 2.1         | 5.94         | 11.8        |
| Sinapupu | 24   | −20.2          | 0.7         | −21.6        | −19.0       | 8.3            | 1.6         | 5            | 10.7        |
| Tuakamali | 43   | −20           | 0.8         | −21.7        | −16.9       | 9.7            | 1.5         | 6.2          | 13.0        |

| Commensals (pig + rat) |
| Kiki  | 29  | −17.8          | 1.9         | −20.7        | −14.1       | 12.5           | 2.1         | 5.94         | 16.1        |
| Sinapupu | 32   | −20.1          | 0.8         | −21.6        | −18.6       | 8.5            | 1.6         | 5            | 10.9        |
| Tuakamali | 56   | −19.8          | 1.1         | −23.0        | −16.9       | 10.1           | 1.7         | 6.2          | 15.0        |

Pig and rat collagen stable isotope results both exhibit statistically significant differences across archaeological phases. When grouped together (i.e., δ¹³C(commensal) and δ¹⁵N(commensal), significant differences are even more apparent. δ¹³C values remain mostly consistent for both pig and rat bone collagen across all three phases. Rat δ¹³C is significantly higher in the Kiki Phase (−17.4 ± 1.9‰) compared to the Sinapupu Phase (−19.7 ± 0.7‰). In the Tuakamali Phase (−19 ± 1.7‰), rat δ¹³C is slightly higher than Sinapupu and still lower than the Kiki Phase, however neither of these differences are
There are no statistically significant differences in pig δ13C across any of the three phases. The likeliest cause of variation in rat δ13C is increased marine dietary inputs in the early Kiki Phase, as δ15Nrat values are also higher during this time. The greater abundance of avifauna in the early Kiki Phase, particularly of roosting seabirds which would exhibit marine-like δ13C and δ15N values, could account for this difference. Rats are known to consume seabird chicks and eggs, and rat access to seabirds has been previously reported as a likely cause for high rat collagen δ15N values in early Pacific archaeological sites [18,27].

Pig, and especially rat, δ15N values vary strongly throughout time periods. Both pig and rat δ15N values are at their highest during the Kiki Phase (9.7 ± 2.1‰ and 13.2 ± 1.3‰, respectively) and then dip to their lowest during the Sinapupu Phase (8.3 ± 1.6‰ and 9.4 ± 1.2‰, respectively). δ15N values for both species then increase again in the Tuakamali Phase (9.7 ± 1.5‰ for pigs and 11.4 ± 1.8‰ for rats). These differences in δ15N values are statistically significant across all three phases for Pacific rat samples, and between the Sinapupu and Tuakamali Phases for pig samples. The lack of statistically significant differences in pig δ15N values between the Kiki and other phases may be driven by the relatively small number of pigs sampled from the Kiki Phase (n = 6). Differences in δ15Ncommensal are statistically significant across all three phases.

4. Discussion

Our data provide novel, semiquantitative evidence for tracking the sustainability and resilience of Tikopia’s agroecosystems across deep time. Changes in commensal δ13C and δ15N values across archaeological phases (Figure 2) reflect anthropogenic transformations of island ecosystems, as well as their subsequent impacts on C and N nutrient flows. This method is only semiquantitative, as changing δ13C and δ15N values do not directly correlate with overall C or N availability. Rather, these results characterize probable sources of nutrient inputs, which can then structure inferences about agroecosystem productivity and sustainability. As commensal δ13C and δ15N are influenced by a range of inextricably linked human, environmental, and physiological factors, accurate characterization requires interpretations that are grounded within specific patterns of human land use and environmental transformations observed on Tikopia.

Previously, rat δ15N values have been shown to consistently decline through time after human arrival on several different Polynesian islands, including Tikopia [18]. While bone collagen of only a single rat specimen from the Tuakamali Phase was included in the previous analysis, that single data point appeared consistent with the declining trend seen on other islands. These new data, which combine additional Tuakamali Phase rat samples with a full sequence of new pig stable isotope data, reveal a novel trend of commensal δ15N declining from the Kiki to Sinapupu Phases, and then rebounding to higher values in the final Tuakamali Phase. We argue that the main driver of this pattern is not direct dietary change, rather transformations to soil N inputs. Differences in quantity and source of soil N inputs would have altered baseline δ15N values, and these changes would subsequently carry up the food chain to commensal species. The lack of change in δ13C values alongside δ15N variability further supports this argument. In other words, our hypothesis is that direct management of island agro-ecosystems by Tikopians transformed island nutrient cycles, and the impacts of these strategies are visible through commensal stable isotope analysis.
The archaeological record from Tikopia speaks to significant transformations to agroecosystem management strategies across the entire island, especially throughout the Sinapupu Phase. During the Sinapupu Phase, commensal $\delta^{15}$N values are at their lowest and the predominant form of agriculture gradually transitioned from “slash-and-burn” or shifting cultivation to the multistory arboricultural system in use today. In this process, the use of fire for agricultural purposes stopped entirely, while the simultaneous intensification of arboricultural practices would have restored a significant amount of forest habitat to areas that were previously under swidden field cultivation. These large-scale changes to the landscape no doubt had rippling effects across the entire social-ecological system. They likely also had significant impacts on shifting island $\delta^{15}$N baselines. The Kiki-Sinapupu transition is consistent with the declining $\delta^{15}$Nrat values observed in other Polynesian islands, and these declines have been explained by the disappearance of $^{15}$N-enriched seabird guano, reduced exploitation of high trophic level marine fauna, and intensified focus on terrestrial C$_3$ landscape productivity [18]. Conversely, the (re)elevated $\delta^{15}$Ncommensal values after the Sinapupu-Tuakamali transition reflect a restoration of forest habitats and their associated fauna, including the return of seabirds and $^{15}$N-enriched guano deposits. The zooarchaeological data support this picture, showing abundant avifauna in the Kiki Phase (NISP = 237), followed by a dramatic reduction in the Sinapupu Phase (NISP = 26), and a partial recovery in the Tuakamali Phase (NISP = 86) [69].

Although $\delta^{15}$Ncommensal values cannot speak directly to nitrogen abundance, they can lend insight into nitrogen flows across the island’s social-ecological system. Tracing nitrogen flows through commensal stable isotope analysis is especially significant, as high N mobility renders it difficult, if not impossible, to investigate past nitrogen abundance through soil analysis. The most readily evident explanation for significant changes in $\delta^{15}$Ncommensal is the loss, and eventual return, of native forest habitat and $^{15}$N-rich natural fertilizers. The return of forest cover may have contributed to increasing $\delta^{15}$N values through altering the forest nitrogen cycle and microbial activity [70]. The loss of some avifaunal species to extinction and extirpation after human arrival to new islands is a common occurrence [71]. In the absence of this steady source of guano fertilization, new sources of nutrient inputs would have perhaps been necessary to maintain shifting
agricultural systems. This pressure would also be heightened under intensified swidden agriculture, particularly with an entire island either already under cultivation or facing the pressures of ever-shortened fallow periods. For example, multidisciplinary research in the Leeward Kohala Field System (Hawai‘i Island) and the dryland agricultural system of Kahikinui (Maui island) both show evidence of a long-term drawdown of available soil nutrients, which suggests these dryland field systems were not sustainable in the long-term without anthropogenic intervention [72–74]. While other forms of traditional agriculture in the Pacific, including irrigated and colluvial slope agriculture, are less extensively studied, they do show higher potential for consistent nutrient rejuvenation through renewed alluvial or colluvial nutrient depositions [75].

Other factors may also have impacted commensal $^{15}$N values. It is possible that rat or pig populations experienced direct changes to their diets, either through changes in the resources available on the landscape (rats) or through direct human intervention in feeding practices (pigs). Pacific rats tend to be opportunistic scavengers with few dietary limitations and small home ranges, thus their diets are assumed to reflect a mix of locally available resources, including meal scraps [76,77]. Changes in $^{15}$Nrat values could reflect reduced access to high trophic level foods. In this case, that would likely equate to reduced consumption of avifauna or marine resources. However, $^{13}$C values would also be expected to decline and rebound alongside $^{15}$N values if marine dietary inputs were driving this trend. This does not appear to be the case for Tikopia rats, though the slightly lower $^{13}$C values in the Sinapupu and Tuakamali periods may reflect reduced access to seabirds, some of which are present only in the Kiki Phase [69].

Pigs are omnivorous much like rats. However, in Pacific contexts pigs were generally kept penned or otherwise restricted from garden areas to prevent destruction of crops [23]. On Tikopia, pig diet does not vary as much as that of rats, and is also appears to be more focused on terrestrial C$_3$ resources with few marine contributions. Pigs also exhibit decreasing dietary variability through time, which has been observed in other stable isotopic studies of commensal fauna in the Pacific, e.g., [14,16,23,78]. Allen and Craig [14] suggest this reduced variability in pig diet on Aitutaki (Cook Islands) may reflect increasing interspecific competition over food resources between pigs and humans, leading up to eventual pig extirpation. Our stable isotope results suggest this process may also have occurred on Tikopia, though complete extirpation of pigs apparently did not occur until late in the Tuakamali Phase [38], and a small pig population was recently reintroduced to Tikopia [31]. Pig $^{13}$C values change very little across all three phases, and do not raise or lower correspondingly with pig $^{15}$N values. This renders it unlikely that changes to $^{15}$N values are a product of fluctuating marine resource inputs. Likewise there are no indications that terrestrial protein sources would have varied across phases. Rather, pig diet appears to be consistently terrestrial, and fluctuating pig $^{15}$N values most likely reflect changes to baseline soil/plant $^{15}$N. The commonality of $^{15}$N trends across both pig and rat populations reinforces our interpretation of island-wide nutrient flow changes (Figure 3).
Figure 3. Scatterplots of bone and tooth dentine collagen $\delta^{13}C$ and $\delta^{15}N$ from (top left) rat (top right) pig and (bottom) combined pig and rat samples across Tikopia’s three primary cultural phases. Commensal dietary isotope values display the lowest $\delta^{15}N$ values and the least variability during the Sinapupu Phase.

Other possible influences on commensal $\delta^{15}N$ values include climatic variability and topographic change. However, oceanic $\delta^{15}N$ baselines remain relatively stable across the studied time period [79,80]. Further, even the gradual decline observed in oceanic $\delta^{15}N$ baselines across time would only account for the Sinapupu Phase “dip” in $\delta^{15}N$ values. This trend would work against the later increases evident in the Tuakamali Phase. Other significant transformations to Tikopia include the emergence of the sandy Ravenga tombolo and subsequent formation of the brackish Te Roto lake. At present it is unclear what, if any, impact this may have had on commensal stable isotope ratios. It is possible that lake formation increased animal reliance on (and access to) fish species, including milkfish (Chanos chanos) that were farmed in the lake. However, these changes mostly occurred very late in Tikopia’s history (the Late Tuakamali and Historic Phases), and probably do not account for the observed commensal isotopic trends. These topographic changes are at least in part a product of extreme cyclone events, which Tikopia has experienced in both recent and long-term history. Cyclone events may also have unpredictable impacts on commensal $\delta^{13}C$ and $\delta^{15}N$, though we expect that on long enough timescales this influence would be negligible.

What then does all of this mean in terms of Tikopia’s sustainability and long-term resilience? The evidence provided by commensal stable isotope ratios suggest that the initial system of forest clearance and slash-and-burn agriculture established in the Kiki Phase was productive for many centuries, though perhaps not sustainable by our definition over the longer term. Commensal $\delta^{15}N$ values declined from the Kiki to the Sinapupu Phase, likely reflecting a gradual depletion of soil N. However, at some point during the Sinapupu Phase a dramatic restructuring of the island’s agro-ecosystem occurred. Slash-and-burn agricul-
ture was eventually replaced by an arboriculturally focused multistory agricultural system which mimicked natural forest cover through replacing native species with introduced crops. This transition is clearest from excavations in the Rakisu agricultural transect [38]. At the same time that there is evidence for this transition, mean $\delta^{15}N_{commensal}$ values return to higher levels, although they do not return to the same values as seen in the Kiki Phase. We argue that this is likely brought about by the return of native forest habitats and renewed N inputs from $^{15}N$-enriched guano. This restructuring speaks to the remarkable resilience of the Tikopia’s social-ecosystem in the ability to adapt, and to recover, following catastrophe or long-term impacts to productivity.

The large-scale transformation of swidden fields and natural forests into intensively managed economic forests is exemplary of “structural substitution” ecomimicry, a strategy which maintains existing ecosystem structure but alters species compositions to increase production of food and other biocultural resources [37]. Ecomimicry strategies as defined by Winter et al. [37] are not ‘one size fits all’ approaches; rather they require flexibility and situational adaptation to the constraints and opportunities presented by local ecosystem structures and services. In return, these strategies tend to be more successful in maintaining species and habitat diversity, while still providing abundant biocultural resources. Uncoincidentally, these strategies are exemplified by place-based traditional Indigenous agriculture. Rather than conceptualizing all forms of human influence on island ecosystems as negative, conservation strategies informed by ecomimicry and biocultural frameworks instead recognize the integral and millennia-long role of humans as engineers of local ecosystems, and examine the impacts that specific actions or behaviors have on long-term ecosystem maintenance and productivity, e.g., [81–83]. In the case of Tikopia, commensal stable isotope evidence suggests that the structural substitution that occurred in the Sinapupu-Tuakamali Phases was a successful long-term adaptation that rejuvenated ecosystem productivity.

In this paper, we take a rather restrictive definition of sustainability (no evidence for soil nutrient drawdown over time) in order to find a quantitative means to evaluate sustainability archaeologically. By this definition, Tikopia does not meet our requirements for sustainability. Realistically, few agro-ecosystems would likely meet our criteria for true ‘sustainability’ in the long term, but this supposition requires further testing. However, the Tikopia case makes a significantly stronger argument for long-term resilience. If the early slash-and-burn agricultural system practiced in the Kiki Phase was unsustainable, it appears that the Tikopia recognized this and reorganized their agro-ecosystem functioning to a form of structural replacement ecomimicry [37]. This transformation evidently resulted in a system that continues to be sustainably managed today.

5. Conclusions

Stable isotope analysis of commensal pig and Pacific rat remains recovered from archaeological sites examines changes to island nutrient flows after human arrival and land use and offers new evidence for sustainability and long-term resiliency on Tikopia Island. Firstly, $\delta^{15}N$ values decline significantly from the Kiki to the Sinapupu Phase, after centuries of forest clearance, settlement expansion, and slash-and-burn agriculture. During the Sinapupu-Tuakamali Phases, the agro-ecosystem was transformed to one dominated by multistory forest arboriculture. This transition is accompanied by higher $\delta^{15}N_{commensal}$ values in the Tuakamali Phase, which indicate a second transformation in nitrogen flows, likely from increased forest cover and renewed guano $^{15}N$ inputs. The later shift to more elevated $\delta^{15}N_{commensal}$ values after initial declines is a pattern that has not yet been seen in any other Pacific island archaeological case study [18]. It demonstrates that adaptability and careful management can lead to millennia of agricultural productivity even on small, relatively isolated islands.

Both past and contemporary datasets speak to the remarkable resiliency—a capability to adapt and restructure in response to large-scale sustainability challenges—of Tikopia’s social-ecological system in the modern era and across millennia. Though the Tikopia case...
study may offer some insights towards global sustainability, it is critical to acknowledge that today the greatest threats to sustainability on Tikopia come not from the Tikopia themselves, but from forces of global climatic change over which they have little control. In 2002, Cyclone Zoe wrought extreme and devastating impacts for Tikopia. Though no lives were lost, all structures on the island were leveled and sources for traditional housing materials lost. The cyclone damaged the lake (Te Roto) that had been supporting freshwater fish populations, and eliminated important ecosystem resources including topsoil, shadecover, and seed dispersers like birds and flying foxes [45]. It has been projected that it will take years for Tikopia to recover to the same levels of self-sufficiency, if a full recovery is even possible. While over the long-term Tikopia has shown itself to be resilient to catastrophe, the frequency and intensity of cyclone events are expected to heighten over the next several decades. Sea level rise, temperature changes, and ocean acidification are other consequences of anthropogenic-induced climate change that pose significant looming threats to Tikopia’s continued resiliency [31,84]. While Tikopia—and ecomimicry strategies more broadly—offer valuable lessons for building more sustainable, resilient social-ecosystems, it may be premature to look towards these alternate templates until we successfully address the known causes of global climate change that already threaten their survival.

**Supplementary Materials:** The following are available online at https://www.mdpi.com/article/10.3390/su13158567/s1, Table S1: Results of stable carbon and nitrogen isotope analysis of commensal bone collagen and quality control indicators, including previously published samples. Table S2: Results of Kruskal Wallis Test for commensal bone collagen \( \delta^{13}C \) and \( \delta^{15}N \) values across archaeological phases. Underlined values are statistically significant (\( p < 0.05 \)). Table S3: Results of Pairwise Mann-Whitney-Wilcoxon Test for pig and rat collagen \( \delta^{13}C \) and \( \delta^{15}N \) values. Underlined values are statistically significant (\( p < 0.05 \)).

**Author Contributions:** Conceptualization, J.A.S., P.V.K. and P.R.; methodology, J.A.S., J.I., S.B., M.L., S.M. and P.R.; formal analysis, J.A.S.; writing—original draft preparation, J.A.S.; writing—review and editing, J.A.S., P.V.K., J.I., S.B., P.R.; visualization, J.A.S.; funding acquisition, P.R. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by the Max Planck Society.

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** ZooMS data can be accessed via Zenodo (doi:10.5281/zenodo.4835792).

**Acknowledgments:** This study was conducted on archaeological collections recovered from Tikopia by Kirch and Douglas Yen in 1977–78, which are now housed at Bishop Museum. Permission to reanalyze the collection was granted through a Destructive Analysis Loan through the Anthropology Department at Bishop Museum. We are grateful to Mara Mulrooney and Charmaine Wong for facilitating access to the collections. P.R., J.I., S.B., M.L. and S.M. thank the Max Planck Society for funding.

**Conflicts of Interest:** The authors declare no conflict of interest.

**References**

1. Fisher, C. Archaeology for Sustainable Agriculture. *J. Archaeol. Res.* 2020, 28, 393–441. [CrossRef]
2. Smith, M.E.; Lobo, J.; Peeples, M.A.; York, A.M.; Stanley, B.W.; Crawford, K.A.; Gauthier, N.; Huster, A.C. The persistence of ancient settlements and urban sustainability. *Proc. Natl. Acad. Sci. USA* 2021, 118. [CrossRef]
3. Toniello, G.; Lepofsky, D.; Lertzman-Lepofsky, G.; Salomon, A.K.; Rowell, K. 11,500 y of human-clam relationships provide long-term context for intertidal management in the Salish Sea, British Columbia. *Proc. Natl. Acad. Sci. USA* 2019, 116, 22106–22114. [CrossRef]
4. Fitzpatrick, S.M.; Erlandson, J.M. Island Archaeology, Model Systems, the Anthropocene, and How the Past Informs the Future. *J. Isl. Coast. Archaeol.* 2018, 13, 283–299. [CrossRef]
5. Kirch, P.V. Three islands and an archipelago: Reciprocal interactions between humans and island ecosystems in Polynesia. *Earth Environ. Sci. Trans. R. Soc. Edinb.* 2007, 98, 85–99. [CrossRef]
6. Leppard, T.P.; DiNapoli, R.J.; Cherry, J.F.; Douglass, K.; Erlandson, J.M.; Hunt, T.L.; Kirch, P.V.; Lipo, C.P.; O’Connor, S.; Pilaar Birch, S.E.; et al. The premise and potential of model-based approaches to island archaeology: A response to Terrell. J. Island Coast. Archaeol. 2021, 1–8. [CrossRef]

7. Vitousek, P.M. Oceanic islands as model systems for ecological studies. J. Biogeogr. 2002, 29, 573–582. [CrossRef]

8. Gómez-Limón, J.A.; Sanchez-Fernandez, G. Empirical evaluation of agricultural sustainability using composite indicators. Ecol. Econ. 2010, 69, 1062–1075. [CrossRef]

9. Hansen, J.W. Is agricultural sustainability a useful concept? Agric. Syst. 1996, 50, 117–143. [CrossRef]

10. Hueting, R.; Reijnders, L. Sustainability is an Objective Concept. Ecol. Econ. 1998, 27, 139–147.

11. Montgomery, D.R. Soil erosion and agricultural sustainability. Proc. Natl. Acad. Sci. USA 2007, 104, 13268–13272. [CrossRef]

12. Pretty, J. Agricultural sustainability: Concepts, principles and evidence. Philos. Trans. R. Soc. Lond. B Biol. Sci. 2008, 363, 447–465. [CrossRef]

13. Marchese, D.; Reynolds, E.; Bates, M.E.; Morgan, H.; Clark, S.S.; Linkov, I. Resilience and sustainability: Similarities and differences in environmental management applications. Sci. Total Environ. 2018, 613–614, 1275–1283. [CrossRef] [PubMed]

14. Allen, M.S.; Craig, J.A. Dynamics of Polynesian Subsistence: Insights from Archaeofauna and Stable Isotope Studies, Aitutaki, Southern Cook Islands. Pac Sci 2009, 63, 477–506. [CrossRef]

15. Guiry, E.J.; Gaulton, B.C. Inferring Human Behaviors from Isotopic Analyses of Rat Diet: A Critical Review and Historical Application. J. Archaeol. Method Theory 2016, 23, 399–426. [CrossRef]

16. Richards, M.P.; West, E.; Rollett, B.; Dobney, K. Isotope analysis of human and animal diets from the Hanamiai archaeological site (French Polynesia). Archaeol. Ocean. 2009, 44, 29–37. [CrossRef]

17. Sheng, P.; Hu, Y.; Sun, Z.; Yang, L.; Hu, S.; Fuller, B.T.; Shang, X. Early commensal interaction between humans and hares in Neolithic northern China—CORRIGENDUM. Antiquity 2020, 94, 1395. [CrossRef]

18. Swift, J.A.; Roberts, P.; Boivin, N.; Kirch, P.V. Restructuring of nutrient flows in island ecosystems following human colonization evidenced by isotopic analysis of commensal rats. Proc. Natl. Acad. Sci. USA 2018, 115, 6392–6397. [CrossRef]

19. Zeder, M.A. Pathways to Animal Domestication. In Biodiversity in Agriculture: Domestication, Evolution, and Sustainability; Cambridge University Press: Cambridge, UK, 2012; pp. 227–259.

20. Luomala, K. The native dog in the Polynesian system of values. In Culture in History: Essays in Honor of Paul Radin; Diamond, S., Ed.; Columbia University Press: New York, NY, USA, 1960; pp. 190–240.

21. Storey, A.A.; Ladefoged, T.; Matiiso-Smith, E.A. Counting your chickens: Density and distribution of chicken remains in archaeological sites of Oceania. Int. J. Osteoarchaeol. 2008, 18, 240–261. [CrossRef]

22. Titcomb, M. Dog and Man in the Ancient Pacific, with Special Attention to Hawaii; Bernice P. Bishop Museum Special Publication; Bishop Museum Press: Honolulu, HI, USA, 1969; Volume 59.

23. West, E.W. An Archaeological Investigation of Pig Husbandry on Tahuata Island, Marquesas, French Polynesia. Ph.D. Thesis, University of Hawaii at Manoa, Honolulu, HI, USA, 2007.

24. Ambrose, S.H. Effects of diet, climate and physiology on nitrogen isotope abundances in terrestrial foodwebs. J. Archaeol. Sci. 1991, 18, 293–317. [CrossRef]

25. Szpak, P. Complexities of nitrogen isotope biogeochemistry in plant-soil systems: Implications for the study of ancient agricultural and animal management practices. Front. Plant Sci. 2014, 5, 103. [CrossRef] [PubMed]

26. van der Merwe, N.J.; Medina, E. The canopy effect, carbon isotope ratios and foodwebs in amazonia. J. Archaeol. Sci. 1991, 18, 249–259. [CrossRef]

27. Swift, J.A.; Miller, M.J.; Kirch, P.V. Stable isotope analysis of Pacific rat (Rattus exulans) from archaeological sites in Mangareva (French Polynesia): The use of commensal species for understanding human activity and ecosystem change. Environ. Archaeol. 2017, 22, 283–297. [CrossRef]

28. Bódí, B.; Takács-Sánta, A. Hardin’s Mistake: Tikopia, the Society That Avoided the Tragedy of the Commons. World Futures 2021, 77, 205–221. [CrossRef]

29. Cowdrey, J.M. Darwinian selection and cultural incentives for resource use: Tikopia as a case study of sustainability. Int. J. Glob. Environ. Issues 2006, 6, 348–361. [CrossRef]

30. Kirch, P.V. Microcosmic Histories: Island Perspectives on “Global” Change. Am. Anthropol. 1997, 99, 30–42. [CrossRef]

31. Mertz, O.; Bruun, T.B.; Fog, B.; Rasmussen, K.; Agergaard, J. Sustainable land use in Tikopia: Food production and consumption in an isolated agricultural system. Singap. J. Trop. Geogr. 2010, 31, 10–26. [CrossRef]

32. Borrie, W.D.; Firth, R.; Spillius, J. The Population of Tikopia, 1929 and 1952. Popul. Stud. 1957, 10, 229–252. [CrossRef]

33. Firth, R.W. We, The Tikopia: Kinship in Primitive Polynesia; Allen & Unwin ltd.: London, UK, 1936.

34. Firth, R.W. Primitive Polynesian Economy; George Routledge and Sons: London, UK, 1939.

35. Quintus, S.; Huebert, J.; Kirch, P.V.; Lincoln, N.K.; Maxwell, J. Qualities and Contributions of Agroforestry Practices and Novel Forests in Pre-European Polynesia and the Polynesian Outliers. Hum. Ecol. 2019, 47, 811–825. [CrossRef]

36. Lincoln, N.K. Agroforestry form and ecological adaptation in ancient Hawai‘i: Extent of the pākukui swidden system of Hāmākua, Hawai‘i Island. Agric. Syst. 2020, 181, 102808. [CrossRef]

37. Winter, K.; Lincoln, N.; Berkes, F.; Alegado, R.; Kurashima, N.; Frank, K.; Pascua, P.; Rii, Y.; Reppun, E.; Knapp, I.; et al. Ecomimicry in Indigenous resource management: Optimizing ecosystem services to achieve resource abundance, with examples from Hawaii. Ecol. Soc. 2020, 25. [CrossRef]
38. Kirch, P.V.; Yen, D.E. Tikopia. The Prehistory and Ecology of a Polynesian Outlier; Bernice P. Bishop Museum Bulletin Honolulu; Bishop Museum Press: Honolulu, HI, USA, 1982.

39. Kirch, P.V.; Swift, J.A. Others New ams radiocarbon dates and a re-evaluation of the cultural sequence of tikopia island, southeast Solomon Islands. *J. Polyn. Soc.* 2017, 126, 313. [CrossRef]

40. McCoy, M.D.; Cervera, C.; Mulrooney, M.A.; McAlister, A.; Kirch, P.V. Obsidian and volcanic glass artifact evidence for long-distance voyaging to the Polynesian Outlier island of Tikopia. *Quat. Res.* 2002, 98, 49–57. [CrossRef]

41. Green, R.C. Lapita. In *The Prehistory of Polynesia*; Jennings, J.D., Ed.; Harvard University Press: Cambridge, UK, 1979; pp. 22–60.

42. Bedford, S.; Spriggs, M.; Regenvanu, R. The Teouma Lapita site and the early human settlement of the Pacific Islands. *Antiquity* 2006, 80, 812–828. [CrossRef]

43. Garanger, J. Incised and applied-relief pottery, its chronology and development in southeastern Melanesia, and extra areal comparisons. In *Studies in Oceanic Culture History Volume 2*; Green, R.C., Kelly, M., Eds.; Pacific Anthropological Records; Bishop Museum Press: Honolulu, HI, USA, 1971; Volume 12.

44. Firth, R.R. *History and Traditions of Tikopia*; The Polynesian Society: Wellington, New Zealand, 1961.

45. Yates, L.; Anderson-Berry, L. The Societal and Environmental Impacts of Cyclone Zoe and the Effectiveness of the Tropical Cyclone Warning Systems in Tikopia and Anuta Solomon Islands: December 26–29, 2002. *Aust. J. Emerg. Manag.* 2004, 19, 16–20.

46. van Doorn, N.L.; Hollund, H.; Collins, M.J. A novel and non-destructive approach for ZooMS analysis: Ammonium bicarbonate buffer extraction. *Archaeol. Anthropol. Sci.* 2011, 3, 281. [CrossRef]

47. Brown, S.; Hebestreit, S.; Wang, N.; Boivin, N.; Douka, K.; Korzow, K. Zooarchaeology by Mass Spectrometry (ZooMS) for bone material-AmBiC protocol v1. *Protocols.io* 2020. [CrossRef]

48. Brown, S.; Douka, K.; Collins, M.J.; Richter, K.K. On the standardization of ZooMS nomenclature. *J. Proteom.* 2021, 235, 104041. [CrossRef]

49. Buckley, M.; Collins, M.; Thomas-Oates, J.; Wilson, J.C. Species identification by analysis of bone collagen using matrix-assisted laser desorption/ionisation time-of-flight mass spectrometry. *Rapid Commun. Mass Spectrom.* 2009, 23, 3843–3854. [CrossRef]

50. Buckley, M.; Gu, M.; Shamer, S.; Patel, S.; Chamberlain, A.T. High-throughput collagen fingerprinting of intact microfaunal remains; a low-cost method for distinguishing between murine rodent bones. *Rapid Commun. Mass Spectrom.* 2016, 30, 805–812. [CrossRef]

51. Prendergast, M.E.; Buckley, M.; Crowther, A.; Frantz, L.; Eager, H.; Lebrasseur, O.; Hutterer, R.; Hulme-Beaman, A.; Van Neer, W; Douka, K.; et al. Reconstructing Asian faunal introductions to eastern Africa from multi-proxy biomolecular and archaeological datasets. *PloS ONE* 2017, 12, e0182565. [CrossRef] [PubMed]

52. Welker, F.; Hajdinjak, M.; Talamo, S.; Jaouen, K.; Dannemann, M.; David, F.; Julien, M.; Meyer, M.; Kelso, J.; Barnes, I.; et al. Palaeoproteomic evidence identifies archaic hominins associated with the Châtelperronian at the Grotte du Renne. *Proc. Natl. Acad. Sci. USA* 2016, 113, 11162–11167. [CrossRef] [PubMed]

53. Katzenberg, M.A. Stable isotope analysis: A tool for studying past diet, demography, and life history. In *Biological Anthropology of the Human Past*; John Wiley & Sons, Inc.: Hoboken, NJ, USA, 2008; pp. 411–441. ISBN 9780470245842.

54. Schoeninger, M.J.; Moore, K. Bone stable isotope studies in archaeology. *J. World Prehistory* 1992, 6, 247–296. [CrossRef]

55. Bender, M.M. Variations in the 13C/12C ratios of plants in relation to the pathway of photosynthetic carbon dioxide fixation. *Phytochemistry* 1971, 10, 1239–1244. [CrossRef]

56. Smith, B.N.; Epstein, S. Two Categories of 13C/12C Ratios for Higher Plants 1. *Plant Physiol.* 1971, 48, 380–384. [CrossRef] [PubMed]

57. Chisholm, B.S.; Erle Nelson, D.; Schwarz, H.P. Stable-Carbon Isotope Ratios as a Measure of Marine Versus Terrestrial Protein in Ancient Diets. *Science* 1982, 216, 1131–1132. [CrossRef] [PubMed]

58. Bocherens, H.; Drucker, D. Trophic level isotopic enrichment of carbon and nitrogen in bone collagen: Case studies from recent and ancient terrestrial ecosystems. *Int. J. Osteoarchaeol.* 2003, 13, 46–53. [CrossRef]

59. Deniro, M.J.; Epstein, S. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim. Cosmochim. Acta* 1981, 45, 341–351. [CrossRef]

60. Minagawa, M.; Wada, E. Stepwise enrichment of 15N along food chains: Further evidence and the relation between δ15N and animal age. *Geochim. Cosmochim. Acta* 1984, 48, 1135–1140. [CrossRef]

61. Austin, A.T.; Vitousek, P.M. Nutrient dynamics on a precipitation gradient in Hawaii. *Oecologia* 1979, 46, 519–529. [CrossRef]

62. Fizet, M.; Mariotti, A.; Bocherens, H.; Lange-Badré, B.; Vandermeersch, B.; Borel, J.P.; Bellon, G. Effect of diet, physiology and climate on carbon and nitrogen stable isotopes of collagen in a late pleistocene anthropic palaeoecosystem: Marillac, Charente, France. *J. Archaeol. Sci.* 1995, 22, 67–79. [CrossRef]

63. Caut, S.; Angulo, E.; Pisau, B.; Ruffino, L.; Faulquier, L.; Lorvelec, O.; Chapuis, J.-L.; Pascal, M.; Vidal, E.; Courchamp, F. Seabird modulations of isotopic nitrogen on islands. *PloS ONE* 2012, 7, e99125. [CrossRef]

64. Richards, M.P.; Hedges, R.E.M. Stable Isotope Evidence for Similarities in the Types of Marine Foods Used by Late Mesolithic Humans at Sites Along the Atlantic Coast of Europe. *J. Archaeol. Sci.* 1999, 26, 717–722. [CrossRef]

65. Swift et al. *ZooMS Data.* 2021. Available online: https://doi.org/10.5281/zenodo.4835792 (accessed on 30 July 2021). [CrossRef]

66. The R Development CORE TEAM, R. Others R: A Language and Environment for Statistical Computing. 2008. Available online: http://softlibre.unizar.es/manuales/aplicaciones/r/fullrefman.pdf (accessed on 30 July 2021).
Abstract: Islands, especially those in Polynesia, have proven effective as ideal "model systems of human evolution and history." However, increased environmental pressures, such as climate change, have highlighted the need to understand the sustainability of these systems. This study examines the environmental context of Tikopia Island, a small and relatively isolated Polynesian outlier in the Southeast Solomon Islands, to investigate pathways to long-term sustainability in a changing world.

Keywords: stable isotopes; archaeology; commensals; nutrient flows; Polynesia; land use; ecomimics; bird remains; waterbird habitat in the face of rising seas.

Sustainability 2021, 13, 8567-8580. https://doi.org/10.3390/xxxxx www.mdpi.com/journal/sustainability

Article
Stable Isotopic Evidence for Nutrient Rejuvenation and Long-Term Resilience on Tikopia Island

Jianxin Hao 1,*, Patrick V. Kirch 1,2, Jana Ilgner 3, Samantha Brown 4, Mary Lucas 3, Sara Marzo 3

1 Institute for Archaeological Sciences, University of Tübingen, 72074 Tübingen, Germany; hao@shh.mpg.de (J.H.); ilgner@shh.mpg.de (J.I.); lucas@shh.mpg.de (M.L.); marzo@shh.mpg.de (S.M.); roberts@shh.mpg.de (P.R.)

2 Department of Anthropology, University of Hawai‘i at Mānoa, Honolulu, HI 96822, USA; kirch@hawaii.edu

3 Institute of Social and Cultural Anthropology, University of Tübingen, 72074 Tübingen, Germany

4 Institute of Archaeology, University of Tübingen, 72074 Tübingen, Germany

* Corresponding author.

Received: date / Revised: date / Accepted: date

Published: date

Publisher’s Note: MDPI stays neutral - no affiliations.

Submitted for possible open access publication under the terms and conditions of the Creative Commons Attribution (CC BY) license (http://creativecommons.org/licenses/by/4.0/).

76. Roberts, M. Origin, dispersal routes, and geographic distribution of Rattus exulans, with special reference to New Zealand. Proc. Natl. Acad. Sci. USA 2006, 103, 11092–11097. [CrossRef]

77. Williams, J.M. The Ecology of Rattus Exulans (Peale) Reviewed. Pac. Sci. 1977, 23, 120–127.

78. Swift, J.A.; Molle, G.; Conte, E. Coastal subsistence and settlement at the Hane dune site, Ua Huka (Marquesas Islands): New insights from Pacific rat (Rattus exulans) stable isotope analysis. J. Archaeol. Sci. Rep. 2017, 15, 161–168. [CrossRef]

79. Sherwood, O.B.; Guilderson, T.P.; Batista, F.C.; Schiff, J.T.; McCarthy, M.D. Increasing subtropical North Pacific Ocean nitrogen fixation since the Little Ice Age. Nature 2013, 505, 78–81. [CrossRef] [PubMed]

80. Wiley, A.E.; Ostrom, P.H.; Welch, A.J.; Fleischer, R.C.; Gandhi, H.; Southon, J.R.; Stafford, T.W., Jr.; Penniman, J.F.; Hu, D.; Duvall, F.P.; et al. Millennial-scale isotope records from a wide-ranging predator show evidence of recent human impact to oceanic food webs. Proc. Natl. Acad. Sci. USA 2013, 110, 8972–8977. [CrossRef]

81. Harman, K.C.; Winter, K.B.; Kurashima, N.; Fletcher, C.H.; Kane, H.H.; Price, M.R. The role of indigenous practices in expanding waterbird habitat in the face of rising seas. Anthroponc. 2021, 34, 100293. [CrossRef]

82. Sato, A.Y.; Ticktin, T.; Alapai, L.; von Allmen, E.I.; Brawner, W.P.I.; Carter, Y.Y.; Carter, K.A.; Keakealani, R.K.; Medeiros, A.C.; Zahawi, R.A. Biocultural restoration of Hawaiian tropical dry forests. Pac. Conserv. Biol. 2021. [CrossRef]

83. Winter, K.; Rii, Y.; Reppun, F.; Hintzen, K.; Alegado, R.; Bowen, B.; Bremer, L.; Coffman, M.; Deenik, J.; Donahue, M.; et al. Collaborative research to inform adaptive co-management: A framework for the He‘eia National Estuarine Research Reserve. Ecol. Soc. 2020, 25. [CrossRef]

84. Rasmussen, K.; May, W.; Birk, T.; Mataka, M.; Mertz, O.; Yee, D. Climate change on three Polynesian outliers in the Solomon Islands: Impacts, vulnerability and adaptation. Geogr. Tidsskr. Dan. J. Geogr. 2009, 109, 1–13. [CrossRef]