



Anthropogenic forests, arboriculture, and niche construction in the Marquesas Islands (Polynesia)

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ABSTRACT

In the Marquesas Islands, topographically rugged and prone to droughts, the subsistence economy at Western contact was strongly focused on arboriculture. Drawing on niche construction theory, we detail the socio-natural processes that gave rise to this cultivation system using the largest Polynesian archaeobotanical study to date. Inceptive, counter-active, and proactive niche construction was evidenced over six centuries of human occupation. Two 13th century tree translocations were identified: candlenut (*Aleurites moluccana*) and breadfruit (*Artocarpus altilis*). Establishment of these and other crops was accompanied by extensive forest clearance and repetitive burning—indicative of shifting cultivation. These activities brought consequential changes to native coastal and lowland vegetation, and extinctions of indigenous forest and bird species. Fifteenth-century counter-active niche construction involved the rapid dispersal and increasing uptake of tree cultivation (especially breadfruit) within and across valleys, and diversification of the tree crop inventory. The advantages of breadfruit cultivation—nutritional, economic, ecological, and geomorphic—were considerable and from the mid-17th century arboriculture came to dominate the Marquesan economy, perhaps accelerated by unpredictable climatic conditions. Six centuries of niche construction created an array of novel selective conditions, invoking evolutionary responses in Marquesan people, flora, and fauna, and fostering a unique ecological inheritance for future generations.

1. Introduction

The development of mutualist, co-evolutionary relationships between humans and other species was fundamental to the emergence of plant and animal domesticates, ultimately giving rise to varied agricultural behaviours and distinctive anthropogenic niches (e.g., Smith, 2016; Zeder, 2017). As O'Brien and Laland (2012) point out, genetic-cultural coevolution was probably more rapid in agricultural societies than in any other context, and had substantial and long-lasting effects. In this study our interests lie with the niche construction (NC) activities that followed the rise of an agricultural lifeway. In particular we examine NC that accompanied island colonisation, the emplacement and dispersal of transported domesticates and associated agricultural practices, and the dynamic human-environment feedback relations that arose over time.

Polynesia is an ideal setting for such an analysis because sustaining human life on small islands necessarily involved early and intensive niche construction activities (Allen, 2013; Quintus and Cochrane, 2018). Human colonists began dispersing into Remote Oceania nearly

three millennia ago (Burley et al., 2015; Rieth and Cochrane, 2015), but movement into East Polynesia was considerably later, from around the 11th to 12th centuries AD (Allen, 2014; Anderson et al., 2019; Kahn and Sinoto, 2017; Kirch, 2017a, 2017b). Relative to islands in the west, those of East Polynesia are typically smaller landmasses and more isolated from one another, but share many features of climate, biogeography, and geology. Settlers in these locations encountered plentiful marine foods but few edible native plants, and high-energy carbohydrates were particularly rare. To insure survival, settlers carried domesticated plant and animal species on their voyages. In the East Polynesian case, some 35 root and tree crops are thought to have been translocated (Whistler, 2009). The lengthy process of transforming island landscapes into productive food-bearing environments began soon after settlement (e.g., Dotte-Sarout and Kahn, 2017; Kirch, 1994; Maxwell et al., 2016; Prebble and Wilmshurst, 2009; Quintus and Cochrane, 2018). However, despite many shared characteristics, Polynesian agricultural economies at Western contact were diverse, varying in content, agro-technologies, and the degree and kinds of socio-cultural investments. Here we document the rise of a strongly

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arboricultural subsistence economy in the Marquesas Islands, an archipelago at the far eastern edge of Polynesia. Our analysis demonstrates that while some important economic trees were among the earliest translocations, the productive anthropogenic forests described by early Europeans arose from several centuries of inceptive, counteractive, and proactive niche construction. Although on present evidence we can only partially address how and why this particular subsistence economy developed, NC theory helps to structure our inquiry and generate further hypotheses.

2. The niche construction framework

Niche construction theory provides a useful framework for investigating the ways that humans have affected and shaped island ecologies through co-evolutionary relationships with biota and landscapes. NC is defined as the “process whereby organisms actively modify their own and each other’s evolutionary niches” (Laland et al., 2016:192; after Odling-Smee et al., 2003). Although recognition of such interactions is long-standing, remarked on by Darwin himself (Laland et al., 2016:195), NC theory formalises the study of these relationships. Matthews et al. (2014:247) suggest two criteria to test for the presence of NC and a third to determine when niche construction has had an effect on evolutionary processes: 1) an organism significantly modifies environmental conditions; 2) these modifications influence selection pressures on recipient organisms; and 3) the modifications lead to evolutionary responses in at least one recipient population (i.e., selective feedback) (see also Laland and Sterelny, 2006). Ultimately the accumulated effects of NC activities, commonly referred to as “ecological inheritance”, give rise to novel selection pressures (Laland et al., 2015; O’Brien and Laland, 2012; Odling-Smee et al., 2003). Odling-Smee and colleagues (2003) differentiate “inceptive” from “counteractive” NC. In the former, organisms initiate a response or change, typically through relocation or perturbation as, for example, migration to new islands or localities. In contrast, counteractive NC involves responses to environmental processes that are already underway (e.g., climate change, anthropogenic modifications). This kind of NC tends to be conservative or stabilizing, and typically is initiated by organisms attempting (intentionally or otherwise) to restore a match between previously evolved features and the changing environment. Both types are relevant to the present analysis, as is the possibility of “proactive” NC, which recognises that humans may actively innovate to solve emergent or anticipated environmental problems or encourage desired outcomes.

Within the natural sciences there is on-going debate over the relative importance of NC activities in evolutionary outcomes, and a questioning of whether NC should be recognised as a separate selection process that parallels natural selection (e.g., Scott-Phillips et al., 2014). Advocates argue the effects of NC are not limited to changes in gene frequencies, and afford significant roles to cultural transmission and selection (Ellis et al., 2016; O’Brien and Laland, 2012). The rapidity of the latter, they argue, render NC a particularly powerful, and previously under-recognised, evolutionary force. O’Brien and Bentley (2015:374) suggest that a NC approach changes the focus of investigation, “from the study of the ecological impact or evolutionary response in a single taxon to the investigation of human eco-evolutionary systems, pathways or networks”. Among the advantages of NC theory we highlight three. Foremost, it focuses on the ecosystem engineering activities of individual organisms, both purposeful and inadvertent, something that has been of considerable importance in human history. Second, it considers not only the benefits (or costs) to the individuals and populations involved in the construction of new niches but also the effects on other biota that share the evolving niche, including domesticates, commensals and wild taxa. Finally, NC theory asks, what are the long-term fitness benefits of particular strategies or decisions? Answering these questions necessarily requires consideration of both ecological and socio-political processes (O’Brien and Laland, 2012), but here we

focus on the former.

In the present study we use charred plant remains, mainly wood charcoal, to track human NC activities and their long-term outcomes in the Marquesas Islands (French Polynesia). Drawing on a large charcoal assemblage, we examine the composition and timing of initial Polynesian plant introductions, and the rate and patterning of the dissemination of arborescent economic taxa across three valleys on Nuku Hiva Island. We also track changes in the abundance, location, and persistence of native woody species that accompanied the spread of Polynesian-introduced trees. Over time, the development of anthropogenic forests gave rise to novel ecosystems, which exerted new selective pressures on both successive generations of humans and on other organisms. In reconstructing these processes, we consider the potential role of external conditions, particularly climate change, which may have fostered counteractive and proactive NC in late prehistory. Finally, we explore some of the known and likely evolutionary responses that arose in recipient populations, both translocated and native. The analysis allows us to outline a co-evolutionary history of Marquesan landscapes, biota, and human agronomic practices, and generate hypotheses for future studies. Understanding the evolution and establishment of tree cropping in this Polynesian island provides new insights into how and why arboricultural economies in general become prominent in some localities and not others, with implications for other global settings.

3. The Marquesas Islands

3.1. Environmental context

The Marquesas Islands are a group of nine high volcanic islands in the central eastern Pacific between 7°5′–10°35′S and 138°30′–140°45′W, approximately 1400 km northeast of the better known Society Islands (Fig. 1). Nuku Hiva, our study site, is the largest island in the archipelago at 340 km². The island is characterised by broad or elongate valleys, enclosed by high ridges with steeply sloping sides (Fig. 2). The valley interiors typically have rich soils, and sometimes sizable permanent streams or rivers, but flat land for agriculture is limited. Cliffs dominate much of the rugged coastline, although small coral reefs and sandy beaches are found in some protected bays.

The Marquesan climate is tropical with minimal seasonal variation; temperatures average 26–27° (Cauchard and Inchauspe, 1978). Precipitation patterns are strongly influenced by island orography, resulting in distinct windward versus leeward regions, with northern coasts being considerably wetter (Fig. 3). In the past, multi-year droughts severely affected Marquesan communities and their cultivation systems, sometimes leading to famines, which occasionally depopulated entire valleys (Crook, 2007; Robarts, 1974). Periods of intense precipitation also occur, sometimes turning streams into raging torrents, uprooting trees, and causing substantial landslides (Robarts, 1974). While such perturbations had some periodicity, their amplitude, duration, and geographic effects were variable and unpredictable (Allen, 2010).

The indigenous vascular flora has a high rate of endemism (Lorence and Wagner, 2011), which made local forests particularly vulnerable to human colonists and their introduced mammalian fauna (domesticated pig and dog, and the Polynesian rat). Some twenty trees, shrubs, and large woody monocots are thought to have been introduced by Polynesian settlers (Table 1), along with several herbaceous plants (Florence, 2004, 1997; Whistler, 2009). Some have been archaeologically identified (Allen and Ussher, 2013; Huebert, 2014; Huebert and Allen, 2016; Millerstrom and Coil, 2008) but several are only known through ethnohistoric sources. Presently commercially-planted coconut groves, dating from the late 19th century, dominate most lowlands areas (Decker, 1991). Well-watered valley bottoms and often steep back-valley slopes are typically forested with secondary vegetation, sometimes including Polynesian introductions and often the

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