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The "regime shift extinctions" hypothesis and mass extinction of waterbirds in Hawai'i

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Abstract

Studies of biodiversity loss commonly imply that species extinctions occurred as a direct result of initial human arrival and thus are attributable to stewardship failures of Indigenous Peoples. However, recent studies have suggested this assumption is not supported by the evidence, prompting a global reevaluation of existing assumptions. To assess the relationship between human arrival in the Hawaiian Islands and documented declines in waterbird biodiversity, we reviewed empirical evidence from paleoecological studies. We first identified the time period that extinct Hawaiian waterbird species were last observed within the fossil record. We then evaluated four hypotheses proposed to explain drivers of Holocene waterbird extinctions: (1) the overkill hypothesis; (2) the deforestation hypothesis; (3) the climate change hypothesis; and (4) the species introductions hypothesis. Of the 18 extinct waterbird species evaluated in this study, 10 were last observed in the fossil record prior to Polynesian arrival, 6 were last observed in the fossil record during the Polynesian era, and 2 were last visually observed after European arrival. Extinctions that possibly occurred during the Polynesian era were likely caused by a suite of factors, some anthropogenic and some non-anthropogenic. Our findings contradict previous studies that attributed Holocene waterbird extinctions to hunting and deforestation by Native Hawaiians and suggest a future line of inquiry regarding a proposed "regime shift extinctions" hypothesis to explain complex impacts of human-mediated and climatic drivers of extinction in the Anthropocene.

KEYWORDS
climate change, deforestation, overkill, paleoecology, species introductions, waterbirds

INTRODUCTION

The role of humans in mass species extinctions has been long debated (Grayson & Meltzer, 2002, 2003; Martin, 1966, 1967), and new theories are still emerging (Fields et al., 2020; Wolfe & Broughton, 2020). While studies suggest that a suite of factors contributed to mass species extinctions (Meltzer, 2015; Ochoa & Piper, 2017; Villavicencio et al., 2015), many studies of biodiversity loss imply they occurred as a direct result of initial human arrival and often examine the loss of biodiversity "since human arrival/settlement" (Carpenter et al., 2020; Flannery, 1990; Miller et al., 2005), implying that anthropogenic factors are the main cause of demise. However, recent studies demonstrate that global mass extinctions in the Holocene disproportionately happened much more recently, at the onset of the 20th century (Ceballos et al., 2015; Waters, 2016), largely due to species introduced during the heightened transcontinental transit associated with European colonization, and technological advancements in hunting such as rifles (Carpenter et al., 2020; Russell & Kueffer, 2019).

Islands are particularly vulnerable to species extinctions, given their reduced land area, gene-flow barriers, and low population sizes (Karels et al., 2008; Manne et al., 1999). Because native island flora and fauna evolved in isolated conditions (e.g., lack of predators and diseases) compared to continental species (Lee, 2011; Pimm, 1991), Holocene extinctions on islands are often directly attributed to first human arrival (e.g., Crowley, 2010; Diamond, 1989; Milberg & Tyrberg, 1993; Steadman et al., 1999). Notable studies published in the last 40 years evaluating biodiversity in the Hawaiian archipelago concluded that Indigenous Polynesians (*Kanaka ʻŌiwi*, Native Hawaiians) directly caused extinctions through hunting and deforestation (e.g., Kirch, 1982; Lewis, 2017; Milberg & Tyrberg, 1993; Olson & James, 1982a, 1984; Perez, 2021; Steadman, 1995).

Four major hypotheses have been proposed regarding the potential causes of extinctions in the Holocene. The first hypothesis proposed in the scientific literature is the overkill hypothesis, originally proposed by Martin (1958, 1967, 1973) as an explanation for the megafaunal extinctions that occurred across multiple continents during the transitional period between the late Pleistocene and the early Holocene. The overkill hypothesis suggests that Indigenous Peoples hunted large megafauna to extinction in North and South America and Africa. Island extinctions are often considered extensions of continental extinctions caused by humans (Burney & Flannery, 2005; Diamond, 1982), and the overkill hypothesis is commonly proposed as a cause of Holocene extinction events on islands, (e.g., Alcover et al., 1998; Crowley, 2010; Duncan et al., 2002; Holdaway, 1989; Wood et al., 2017), including the Hawaiian Islands (e.g., Olson & James, 1982a, 1984; Steadman, 1995).

The deforestation hypothesis suggests that species extinctions in the Holocene occurred due to the destruction of forest habitat by Indigenous Peoples (Bussell, 1988; Holdaway, 1989; Milberg & Tyrberg, 1993) and is often applied to island systems, which have experienced high rates of forest species extinctions (Sodhi, Wilcove, Lee, et al., 2010; Sodhi, Wilcove, Subaraj, et al., 2010). In the Hawaiian Islands, studies over the last 40 years have attributed avian extinctions that occured during the Holocene to the clearing of forests by Native Hawaiians for agriculture (e.g., Kirch, 1982; Olson & James, 1984; Steadman, 1995).

The climate change hypothesis was first proposed as an alternative in continental systems to the overkill hypothesis (Grayson & Meltzer, 2002, 2003; Lima-Ribeiro & Diniz-Filho, 2017; Louys et al., 2021; Stewart et al., 2021), suggesting that the change in climate from the Pleistocene to the Holocene was too severe for megafauna to survive, causing a mass extinction event (Grayson, 1987; Meltzer, 2015) and/or changes in habitats of megafauna that altered their diet and migration patterns (Meltzer, 2015; Seersholm et al., 2020; Villavicencio et al., 2015). The climate change hypothesis has been applied to Holocene island extinctions as well (Ochoa & Piper, 2017; Virah-Sawmy et al., 2010), including the Hawaiian Islands (Athens, 1997; Pau et al., 2012). These studies suggest that changes in rainfall caused shifts in forest vegetation, which were ultimately responsible for forest species extinctions.

Species introductions by humans, including by Indigenous Peoples (Roff & Roff, 2003; Wood et al., 2017), have potentially caused more island extinctions in the Holocene than overhunting or deforestation (e.g., Louys et al., 2021). While the species introductions hypothesis has largely focused on plants and animals, it could be applied to viruses as well. For example, the virus that caused a bird flu outbreak (e.g., Stokstad, 2022) was introduced through human-introduced or migratory birds. Indeed, introduced avian diseases have caused declines of millions of native, resident birds globally (Hvistendahl, 2015; Szabo et al., 2012). Studies in the Hawaiian Islands have used subfossil remains and pollen samples from soil cores to propose that introduced rodent species (i.e., rats) were responsible for both shifts in species assemblages of forests and avian predation that presumably led to avian extinctions during the Holocene, rather than overhunting and deforestation by Native Hawaiians (Athens et al., 2002; Athens & Ward, 1993). Similarly, the introduction of avian malaria and mosquitoes in the 1800s is well known to have caused dramatic declines in forest bird species (Atkinson & LaPointe, 2009; van Riper, 1986).

Each of the hypotheses for mass avian extinctions in the Hawaiian Islands—the overkill hypothesis, the deforestation hypothesis, the climate change hypothesis, and the species introductions hypothesis—has been individually criticized as inadequate to fully explain mass avian extinctions in the Hawaiian Islands (e.g., Athens et al., 2002; Olson & James, 1984; Pau et al., 2012). Fossils of large species with hard parts are more likely to be discovered than fossils of small species lacking hard parts (Milberg & Tyrberg, 1993), so paleoecological studies pertaining to avian extinctions in Hawaiʻi have primarily focused on large, flightless land birds, hereafter referred to as "waterbirds." Present-day populations of Hawaiian waterbirds are conservation-reliant (Reed et al., 2012), meaning that they are at risk from threats so persistent that they require continuous management to maintain population levels above those that would trigger listing as threatened or endangered under the Endangered Species Act (Scott et al., 2005).

Here, we first use empirical evidence from the fossil record and observational data to identify the potential timing of waterbird extinctions in the Hawaiian Islands. We then present an overview of evidence from the existing literature associated with each of the four proposed hypotheses for the drivers of waterbird extinctions in the Hawaiian Islands during the Holocene: (1) the overkill hypothesis; (2) the deforestation hypothesis; (3) the climate change hypothesis; and (4) the species introduction hypothesis.

METHODS

Extensive literature searches were performed using search engines (Google Scholar and Web of Science). We first reviewed paleoecological data on waterbird extinctions in the Hawaiian Islands by searching for the literature on subfossil remains of waterbirds, as well as direct observations of waterbirds that are now considered extinct. Search terms included "waterbird," "fossil," "extinction," and "Hawai'i." We also referred to published books on avian extinctions in the Hawaiian Islands and cross-checked our results with the AVOTREX database, which reports morphometric trait information for 160 bird species known to have gone extinct in the last 130,000 years (Sayol et al., 2025).

To evaluate the overkill hypothesis, we used combinations of search terms such as "overkill," "waterbird," "Hawai'i," "midden," and "fossil" to search for the literature that provided evidence dating prior to European arrival of human consumption and/or human use of waterbirds. We considered the literature that reported on waterbird subfossil remains found within human middens and took particular note of subfossils that were reported to have been altered by humans. We reviewed paleoecological evidence for the deforestation hypothesis by using combinations of search terms such as "deforestation," "pollen," "charcoal," "Hawai'i," "spore," and "fossil" to search for the literature that examined pollen samples of forest species in combination with charcoal samples from soil cores, as peaks in charcoal are often representative of local fires and in combination with pollen samples, can be used to infer forest clearance by humans (Byrne & Horn, 1989; Piperno, 1990). To review evidence for the climate change hypothesis, we used search terms such as "pollen," "climate," "rainfall," "Hawai'i," and "fossil" to search for paleoecological studies that examined changes in pollen species in combination with changes in climate, as pollen and climate data from the same sites would provide the strongest evidence for the climate change hypothesis. Moreover, we focused our search on studies of localized changes in climate, as local climate factors (e.g., rainfall) vary spatially in the Hawaiian Islands (Giambelluca et al., 2013).

We reviewed evidence for the species introductions hypothesis by using combinations of search terms such as "waterbird," "fossil," "introduction," "species," "vertebrate," "pollen," "disease," and "Hawai'i" to search for the literature containing paleoecological data on species introductions that occurred prior to European arrival. We focused on introductions of vertebrate species, given their potential impacts on waterbirds via predation, competition, or habitat alteration. We noted literature that contained subfossil remains of introduced species and waterbird species found within the same soil layers, as well as paleoecological studies that reported changes in pollen species correlated with the presence of subfossils of introduced species. We also searched for the literature that examined diseases brought by introduced species as an explanation for waterbird extinctions.

RESULTS

Waterbird extinctions

A search for waterbird extinctions in the Hawaiian Islands returned 11 sources that contained data on 27 waterbird species that have gone extinct from the islands of Kaua'i, O'ahu, Maui, Moloka'i, Hawai'i, Kauō (Laysan Island), and Pihemanu (Midway Atoll) (Table 1). Using the most recent estimates for Polynesian arrival of ~800–1000 years B.P. (Kirch, 2011), evidence suggests that 10 waterbird species were last observed in the fossil record prior to Polynesian arrival (>1000 years B.P.), and 6 were last observed in the fossil record during the Polynesian era (Figure 1a). Published observations of two waterbird species state they were last visually observed after European arrival, ~80 years B.P. Subfossils of nine extinct waterbird species were either not dated in the literature or dates were ambiguous and thus were not evaluated for this study. Seven extant waterbird species were also observed in the fossil record.

Overkill hypothesis

Four papers collectively described subfossil remains of four extinct waterbirds within human middens, discovered at five different sites on three different islands

TABLE 1 Timeline of last observations of Hawaiian waterbirds in the fossil record or visually.

Species	Date of last observation (years. B.P.)	References
Greater Hawaiian Goose (*Branta hylobadistes*)	Unreported	Olson and James (1984), (1991), James et al. (1997)
Large O‘ahu Goose (*Branta* aff. *hylobadistes*)	Unreported	Olson and James (1982b), (1984), (1991)
Medium Kaua‘i Goose (*Branta* aff. *hylobadistes*)	5145–6740	Olson and James (1982b), (1984), (1991)
Kaua‘i Turtle-Jawed Goose (*Chelychelynechen quassus*)	5145–6740	Olson and James (1982b), (1991), Burney et al. (2001)
Giant Hawai‘i Goose (*Geochen rhuax)*	500–900	Wetmore (1943), Olson and James (1982b), (1991)
Large Hawai‘i Goose[a]	Unreported	Olson and James (1982b), (1991)
Supernumerary O‘ahu Goose	770 ± 70	Olson and James (1982b), (1984), (1991)
Maui Nui Moa-Nalo (*Thambetochen chaliodous*)	4340 ± 610	Olson and Wetmore (1976), (1984), (1991), James et al. (1987)
O‘ahu Moa-Nalo (*Thambetochen xanion*)	770 ± 70	Olson and James (1982b), (1984), (1991), James et al. (1987), Athens et al. (2002)
Stumbling Moa-Nalo (*Ptaiochen pau*)	Unreported	Olson and Jams (1984), (1991)
Undescribed long-legged duck (*Tadorna sp.*)	Unreported	Burney et al. (2001)
Kaua‘i Mole Duck (*Talpanas lippa*)	5145–6740	Olson and James (1982b), Burney et al. (2001)
Moloka‘i Flightless Ibis (*Apteribis glenos*)	5245–5510	Olson and Wetmore (1976), (1982b), (1984), (1991)
Maui Flightless Ibis (*Apteribis brevis)*	1850 ± 270	Olson and Wetmore (1976), (1982b), (1984), (1991), James et al. (1987)
Maui Flightless Ibis (*Apteribis sp.*)	1850 ± 270	Olson and James (1991), (1976)
Lāna‘i Flightless Ibis (*Apteribis sp.*)	700–1100	Dove and Olson (2011)
Hawaiian Rail (*Porzana sandwichensis*)	80	Olson and James (1982b), (1991), Athens et al. (1991)
Larger Hawaiian Rail (*Porzana sp.*)	Unreported	Olson and James (1982b), (1991)
Medium Kaua‘i Rail (*Porzana* sp.)	5145–6740	Olson and James (1982b), (1984), (1991)
Large Kaua‘i Rail (*Porzana* sp.)	5145–6740	Olson and James (1982b), (1984), (1991)
Ziegler‘s Crake (*Porzana ziegleri*)	770 ± 70	Olson and James (1982b), (1984), (1991), James et al. (1987)
Moloka‘i Crake (*Porzana menehune*)	5245–5510	Olson and James (1982b), (1984), (1991)
Kepler‘s Crake (*Porzana keplerorum*)	Unreported	Olson and James (1984), (1991), James et al. (1987)
Medium Maui Rail (*Porzana* sp.)	Unreported	Olson and James (1982b), (1984), (1991)
Ralph‘s Crake (*Porzana ralphorum*)	770 ± 70	Olson and James (1982b), (1984), (1991), James et al. (1987)
Severn‘s Crake (*Porzana severnsi*)	Unreported	Olson and James (1982b), (1984), (1991)
Laysan Rail (*Porzana palmeri*)	80	Walther (2016)
Ae‘o (Hawaiian Stilt - *Himantopus mexicanus knudseni*)	Extant	Burney et al. (2001)
‘Alae ‘ula (Hawaiian Gallinule - *Gallinula galeata sandvicensis*)	Extant	Olson and James (1982b)
‘Alae ke‘oke‘o (Hawaiian Coot - *Fulica alai*)	Extant	Burney et al. (2001)
Nēnē (Hawaiian Goose - *Branta sandvicensis*)	Extant	Burney et al. (2001)
Koloa maoli (Hawaiian Duck - *Anas wyvilliana*)	Extant	Burney et al. (2001)
‘Auku‘u (Black-crowned Night Heron - *Nycticorax nycticorax hoactli*)	Extant	Burney et al. (2001)
Koloa pōhaka (Laysan Duck - *Anas laysanensis*)	Extant	Burney et al. (2001)

[a]Different from *Branta* and *Geochen*.

(McCoy & Gould, 1977; Olson & James, 1982b; Haun, 1986; Athens et al., 1991; Figure 2). Of the four subfossils of extinct waterbird species discovered, none exhibited signs of human alteration—cut marks or charred bone—but were found within the same sites as cooking tools, providing correlative evidence of potential human use. The only subfossils described in the literature as having charred bones belonged to an unidentified

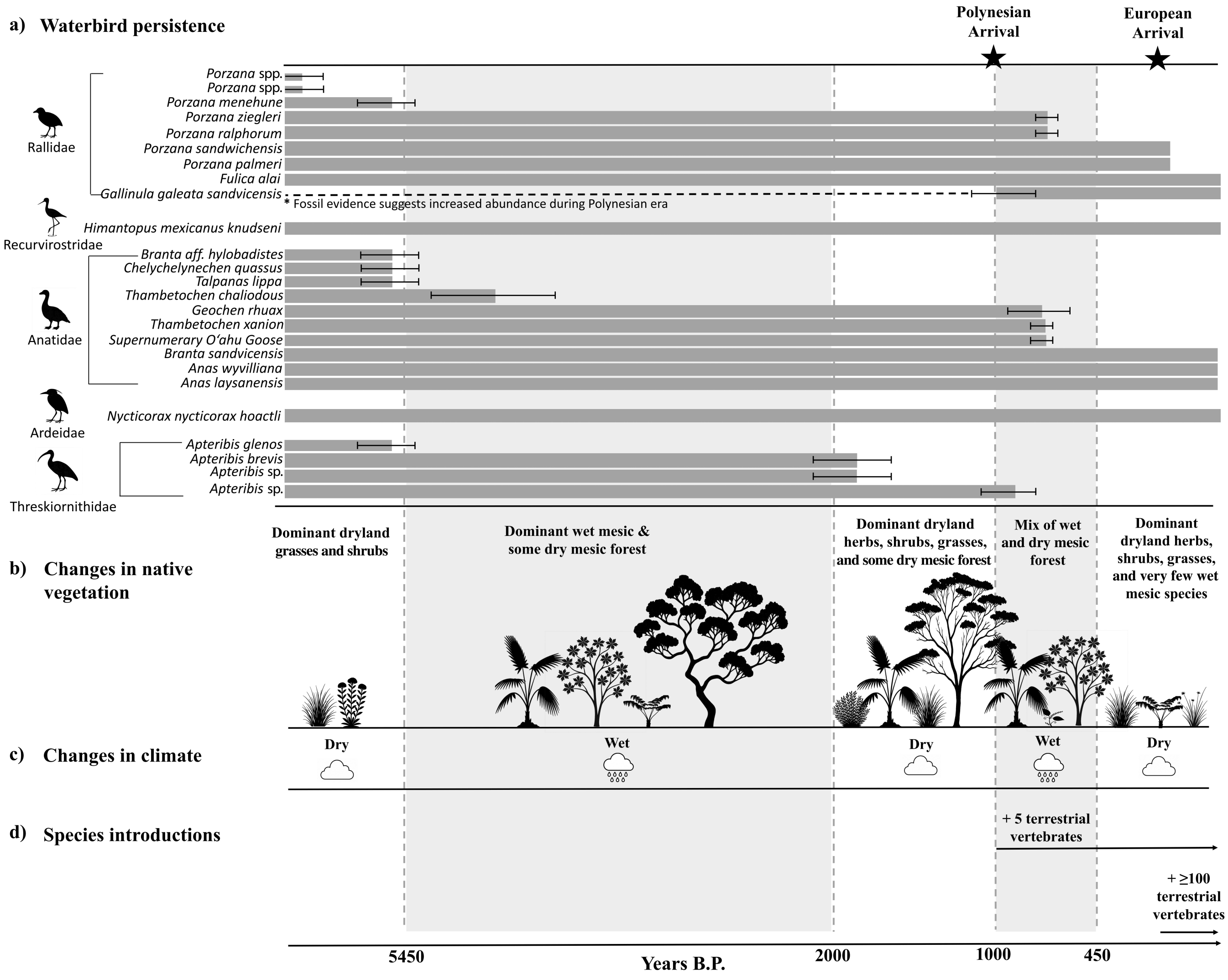
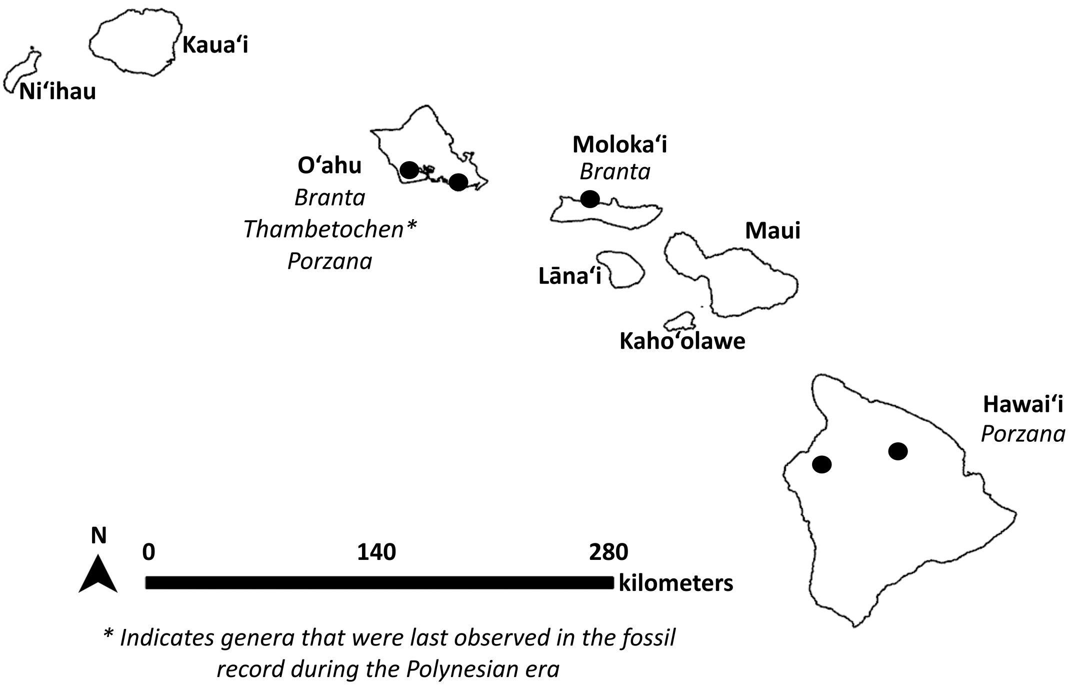


FIGURE 1 A general timeline of (a) persistence of Hawaiian waterbirds based on dated fossils and visual observations; (b) changes in native vegetation; (c) changes in climate; (d) introduced species. Gray dotted lines indicate a proposed ecological regime shift. Images within this figure were created using OpenAI.

goose species in the genus *Branta*. As a waterbird species in the genus *Branta* is still extant today (*Branta sandvicensis*), it cannot be confirmed if those subfossils were from an extinct waterbird species. Furthermore, at one of the sites (Kalaeloa–Barber's Point), the authors noted that dating of subfossils was challenging (Olson & James, 1982b). Further, Rieth and Athens (2013) suggest that the hearth was likely placed within or on top of the sinkhole soils that contained fossil remains of older waterbird species and was likely not associated with human consumption of waterbirds.

Deforestation hypothesis

Five papers were found that examined pollen samples in combination with charcoal samples, providing evidence for changes in forest vegetation due to human activity since Polynesian arrival (Athens & Ward, 1993; Athens et al., 1992, 2002; Burney et al., 1995; Pau et al., 2012). All five papers suggest that native forests continued to persist well after Polynesian arrival. Evidence from a low elevation site on Maui suggests that native forests continued to persist even with an increase in fire activity after Polynesian arrival (Pau et al., 2012), and evidence from a lowland region on O'ahu and a high elevation bog on Maui shows no increase in fire activity during the estimated time of Polynesian arrival (Athens & Ward, 1993; Burney et al., 1995). Furthermore, even in sites where pollen of some forest species began to decline during the Polynesian era, charcoal particles were in extremely low abundance, suggesting the forest losses were not due to anthropogenic fires (Athens & Ward, 1993; Athens et al., 1992, 2002).



** Indicates genera that were last observed in the fossil record during the Polynesian era*

FIGURE 2 Map of evidence considered regarding the overkill hypothesis. Solid circles represent where subfossils of Hawaiian waterbird genera were found within human middens. An asterisk indicates a genus that was last observed in the fossil record during the Polynesian era.

Climate change hypothesis

Two papers examined changes in pollen species in combination with rainfall patterns since the early Holocene (Figure 1b,c). Evidence from these papers suggested that prior to human arrival the Hawaiian Islands experienced multiple changes in vegetation composition due, at least in part, to climate change. Burney et al. (1995) examined pollen samples found in soil cores within a high elevation bog on Maui that dated back ~9400 B.P. Analysis indicated that dominant vegetation consisted of dryland grass species ~9400 B.P., which began to decline ~5750 years B. P. Then, a few hundred years later ~5450 B.P., the dominant understory vegetation shifted from grasses to wet mesic fern species. Vegetation then shifted to a mix of wet mesic and dryland grasses, sedges, trees, and shrubs ~2190 B.P. These changes in vegetation correlated with changes in concentrations of the trace metals cadmium, copper, lead, and zinc, suggestive of shifts in rainfall. Pollen samples on Maui analyzed by Pau et al. (2012) indicated a shift in vegetation from primarily a mix of dry forest, herb, and grass species ~2253 years B.P. to primarily a mix of wet mesic forest species ~973 years B.P. The wet mesic forest persisted, but some wet mesic species declined until ~451 years B.P., at which point there was an increase in dryland herb and grass species. Their analysis also indicated a correlation between shifts in vegetation and changes in rainfall.

Species introductions hypothesis

Three papers described subfossils of vertebrate species introduced by Polynesians and now-extinct native waterbird species found within the same soil layers. One of these papers also examined changes in pollen species in combination with subfossil remains of a vertebrate species introduced by Polynesians. Evidence from all the four papers indicated that the Pacific rat (*Rattus exulans*) inhabited areas concurrently with Hawaiian waterbirds (Athens et al., 1991, 2002; Burney et al., 2001; Figure 1d). Subfossil evidence from Burney et al. (2001) suggested that Hawaiian waterbirds also inhabited areas with domesticated vertebrate species introduced by Polynesians, such as chickens (*Gallus gallus*), dogs (*Canis familiaris*), and pigs (*Sus scrofa*), as well as migratory shorebirds. Evidence from subfossil remains and pollen samples indicated that the introduction of the Pacific rat occurred concurrently with declines in lowland dry forest vegetation, particularly *loulu* (*Pritchardia* spp.; Athens et al., 2002; Figure 1d). Notably, no sources have explored the possible role of avian viruses relating to waterbird extinctions in Hawai'i, despite introduced diseases, which are often vectored by introduced animals, having known major impacts on waterbird populations (Hvistendahl, 2015; Stokstad, 2022; Szabo et al., 2012) and other avian species in Hawai'i (Atkinson & LaPointe, 2009; van Riper, 1986).

DISCUSSION

Our literature review suggests that extinctions of waterbirds in the Hawaiian Islands were likely caused by a combination of climate change and species introductions, rather than overhunting and deforestation by Indigenous Peoples. These results stand in contrast to inferences from previous studies (e.g., Boyer, 2008; Kirch, 1982; Milberg & Tyrberg, 1993; Olson & James, 1982a, 1984; Scott et al., 2001; van Rees & Reed, 2014; van Riper & Scott, 2001). Our findings are consistent with global evidence that climate change and species introductions were, in many cases, the primary drivers of Holocene extinctions. These causes were exacerbated by additional species introductions (e.g., cats and rodents), hunting, and habitat alteration in the European colonization period (Burney et al., 2021; Johnson & Stattersfield, 1990; Nogués-Bravo et al., 2008), leading to further extinctions.

Our results add to a growing body of the literature suggesting paleoecological data should be used with caution when drawing conclusions about historical ecology, particularly the attribution of extinction events to Indigenous Peoples. While paleoecological data may provide insights into historical ecology, the fossil record provides a biased view of past faunas, because bones of species differ in their accumulation rate and capacity for preservation (Holland, 2016), and tropical environments lend themselves to rapid decay, reducing the likelihood that fossils will form (McAdams et al., 2021; Morley & Goldberg, 2017; Stephens et al., 2017). In many cases, species persist past their last occurrence in the fossil record (Haile et al., 2009; Graham et al., 2016; Wang et al., 2021), and Hawaiian waterbirds are likely no exception. For example, Burney et al. (2001) discovered fossils of the extant *ʻAlae keʻokeʻo* (Hawaiian Coot – *Fulica alai*), *Nēnē* (Hawaiian Goose – *Branta sandvicensis*), and *Koloa pōhaka* (Laysan Duck – *Anas laysanensis*) in soil layers dated before and during the Polynesian era; however, they were not observed in soil layers dated after the Polynesian era. Out of the six waterbird species that were last observed in the fossil record during the Polynesian era, subfossils were observed on the islands of Oʻahu and Hawaiʻi (Athens et al., 1991; Haun, 1986; McCoy & Gould, 1977; Olson & James, 1982b). The lack of fossil evidence from other islands could be due to challenges with discovering fossils or limitations of fossil formation (Gardner et al., 2016; Holland, 2016). However, it is also possible that no waterbird extinctions occurred during the Polynesian era on other islands. Moreover, dating of subfossils can be challenging (Olson & James, 1982b, 1984, 1991, Rieth and Athens 2013). Nine waterbird subfossils were either not associated with radiocarbon dates in the literature or the dates provided were ambiguous, as highlighted in Rieth and Athens (2013).

The available evidence does not support the notion that Native Hawaiians overhunted waterbird species to extinction, consistent with recent continental studies focused on megafauna extinctions (Grayson & Meltzer, 2002). First, our results show that, in the Hawaiian Islands, no extinct waterbird remains have been observed in an archaeological midden. Second, distinguishing between bones derived from human use and death from other causes is challenging, particularly without the presence of cutmarks or evidence of cooking. Even traces of burning can be misleading, as they could be attributed to natural fires rather than manipulation by humans (Haynes, 2007). Furthermore, skeletal elements or carcass segments rarely remain at the original kill sites, and preservation is often poor at dispersed household camps containing segments of skeletons and fragmented bones (O'Connell et al., 1992). Importantly, the limited number of faunal fossil remains found within human archaeological sites in the Hawaiian Islands should not be considered sufficient on its own to form conclusions regarding overconsumption of a species by Indigenous Peoples.

Evidence suggests that changes in forest habitat during the Polynesian era were not likely caused by burning and clearing of forests by Hawaiians for agriculture, as has been suggested over the last 40 years (e.g., Kirch, 1982, 1985; Olson & James, 1982a, 1984). This interpretation is consistent with the models by Gon et al. (2018), which suggest that less than 15% of native terrestrial ecosystems were altered by Native Hawaiians, compared to over 50% that were altered or lost since European arrival. Indeed, pollen analyses from some sites in our synthesis indicated declines in *loulu* forests at the very onset or immediately prior to Polynesian arrival. Furthermore, contrary to commercial agriculture that tends to destroy the habitat types that native birds depend on (Benton et al., 2021), Indigenous stewardship approaches and associated agroecology practices often protected and expanded forest and wetland habitats in the Hawaiian Islands (Lincoln et al., 2023; Winter et al., 2018, 2020). While this review was focused on waterbird extinctions, the lack of evidence for deforestation by Native Hawaiians has implications for other Holocene avian species extinctions that occurred in the Hawaiian Islands prior to European arrival, which have previously been attributed to Native Hawaiians (e.g., Boyer, 2008; Olson & James, 1982a).

While the climate change hypothesis was primarily explored as an alternative explanation to the deforestation hypothesis, other environmental variables could have resulted in ecological shifts that impacted waterbird survival. For example, during a Pleistocene interglacial period, sea levels rose high enough to cover not only all the coastal wetlands in the entire archipelago, but also the land bridge that once connected Maui, Molokaʻi, Kahoʻolawe, and Lānaʻi, separating the islands ~400,000–100,000 years B.P. (Price & Fisk, 2004). The complete loss of Maui Nui's coastal wetlands undoubtedly had significant impacts on the population size of waterbirds, and the separation of these islands would have limited the dispersal and the gene flow of flightless waterbirds, such as the moa-nalo and Maui Flightless Ibises. Similarly, subsequent changes in sea level in the Hawaiian Islands during the Holocene (Jones, 1993) would have created declines in wetland habitat, which may have been so significant that they could no longer support viable breeding populations of flightless land birds. Scientific publications in the last 40 years have claimed that Native Hawaiians caused declines in dry lowland forest vegetation through forest clearing (Kirch, 1982; Olson & James, 1982a, 1984). However, the evidence from lowland regions on the islands of Maui and Oʻahu indicates that the shift from dry to wet dominant vegetation was correlated with reduced rainfall that occurred ~200 years prior to Polynesian arrival in these regions. Evidence also suggests that both dry and wet forest species continued to persist until European arrival. Thus, shifts in vegetation are more likely due, at least in part, to changes in climate.

A small number of species introductions by Hawaiians likely played a large role in some waterbird extinctions. Subfossils of the Pacific rat (*R. exulans*), an invasive species throughout Oceania, have been found within the same soil layers as extinct Hawaiian waterbirds. While the primary diet of the Pacific rat is insects, plant matter, and seeds (Shiels & Drake, 2011, 2015; Sugihara, 1997; Wirtz, 1972), the species will secondarily depredate vertebrates, particularly when there is a decrease in primary food sources (Fleet, 1972). The Pacific rat is known to depredate eggs, chicks, and adults of large ground-nesting seabirds that have not evolved an adequate defense against this predator (Fleet, 1972; Kepler, 1967; Wirtz, 1972), as was likely the case for ground-nesting waterbirds. As such, the Pacific rat may have been a predator of Hawaiian waterbirds, although the Pacific rat reportedly coexisted in the last century with the now-extinct *Moho* (Hawaiian Rail, *Porzana sandwichensis*), as well as another extinct Pacific Island waterbird, the Wake Island rail (*Gallirallus wakensis*; Olson, 1999)—both of which persisted until the 20th century.

The Pacific rat also may have had indirect impacts on avian diversity and abundance. For example, the Pacific rat was likely a major contributor to declines in forest vegetation (Holdaway, 1989; Hunt, 2007; Roff & Roff, 2003). Indeed, islands without the Pacific rat, such as Huelo islet off the coast of Molokaʻi, are dominated by *loulu* (Athens et al., 2002), in contrast to islands with the Pacific rat, such as Mōkapu islet, adjacent to Huelo off the coast of Molokaʻi, which have very few *loulu* (Athens et al., 2002). A portion of the Pacific rat's diet is large seeds (Shiels & Drake, 2011, 2015; Wirtz, 1972). Once consumed, seeds that pass through the digestive tracts of rats have a very low chance of viability (Perez et al., 2008). Upon introduction, the Pacific rat had few predators, little competition for resources, and high fecundity (Kramer, 1971). Thus, as subfossils of the Pacific rat have been discovered across the Hawaiian Islands (McDermott et al., 2000), it is likely that this species had widespread impacts on native lowland forest, including inducing a transition from a forest dominated by large-seeded tree species to one dominated by small-seeded trees (Athens et al., 2002) which would have had cascading effects on associated avian diversity.

Rats are not the only non-native species to impact bird diversity. Polynesian-introduced chickens may have competed with ground-foraging waterbirds, such as rails, for food resources. They may have also transmitted diseases to waterbirds, as avian diseases from introduced species are known drivers of other Hawaiian avian extinctions (van Riper, 1991; Warner, 1968). Avian diseases could have also been transmitted by migratory birds, which are present within the fossil record at the same time as some extinct waterbird species (Burney et al., 2001). However, there are no studies in the Hawaiian Islands that have produced evidence to test hypotheses relating to the introduction of new virus species, such as bird flu, via the vector of migratory birds.

In the contemporary era, dogs and pigs are known to depredate and/or destroy extant Hawaiian waterbird nests (Berger, 1981; Harmon, Wehr, & Price, 2021), and feral pigs are known to have detrimental impacts on forest vegetation by altering microbial communities (Cuddihy & Stone, 1990); however, prior to European contact, both dogs and pigs were husbanded by Hawaiians as domesticated animals in enclosures. It was not until European arrival, and the subsequent suppression of Indigenous stewardship, that these species were able to roam as feral animals (Luat-Hūʻeu et al., 2021). Thus, the potential for dogs and pigs to impact Holocene waterbird extinctions, while possible, seems unlikely. While somewhere between 24 and 62 plant species were introduced by Hawaiians (Gon et al., 2018), they were not the focus of this paper, as they were largely agricultural crops that did not naturalize readily into surrounding native wetland ecosystems, with the exception of *Hau* (*Hibiscus tiliaceus*).

While some vertebrate species were introduced by Hawaiians, most vertebrate introductions occurred after European arrival. Indeed, at least 100 terrestrial vertebrate species have been introduced since European arrival (Lohr, 2012). These include two additional species of rats (*Rattus* spp.), cats (*Felis catus*), small Indian mongooses (*Herpestes auropunctatus*), American bullfrogs

(*Lithobates catesbeianus*), cane toads (*Rhinella marina*), barn owls (*Tyto alba*), and cattle egrets (*Bubulcus ibis*), all of which are known predators of Hawaiian waterbirds (Eijzenga, 2009; Harmon, Wehr, & Price, 2021). European-introduced mammals were likely responsible for the extinctions of three Hawaiian rail species (Olson, 1999; Walther, 2016) and have been a major contributor to the decline of extant Hawaiian waterbird populations (Christensen et al., 2021; Harmon, Wehr, & Price, 2021). Indeed, mammalian predators introduced to the Hawaiian Islands by Europeans—Norway rats, black rats, cats, and the small Indian mongoose—pose the greatest threat globally to endangered species, particularly avian species (Duenas et al., 2021).

There are alternative explanations for Hawaiian waterbird extinctions that have yet to be formally proposed. One of these relates to avian diseases (e.g., bird flu) that have the potential to decimate bird populations. While disease is sometimes mentioned as a cause of extinction in the literature, it is not considered nearly as often as the four hypotheses explored in this review. However, avian diseases from migratory species have caused massive declines in native, resident species (Hvistendahl, 2015; Szabo et al., 2012). During the time period prior to Polynesian arrival, which was dominated by wet mesic forest, ephemeral ponds would have been more abundant and could have temporarily increased the number of migratory shorebirds and waterbirds and thus increased the potential for transmission of avian diseases to endemic waterbird species. Indeed, ephemeral ponds provide temporary habitat for migratory waterbirds in the Hawaiian Islands today (Paxton et al., 2021). Furthermore, changes in climate could have created conditions more or less conducive to the spread of disease, as has been observed in recent years (Liao et al., 2017).

Another alternative explanation for waterbird extinctions relates to the concept of regime shifts (Folke et al., 2004, 2010). An ecological regime shift is a persistent shift in the structure and dynamics of an ecosystem that results from a change in the internal feedback and processes within the system. This shift is typically driven by a large, abrupt external disturbance (e.g., volcanic eruption) or persistent directional changes (e.g., climate changes; Biggs et al., 2012), or both. We note that other terms have been used to describe this transition, such as critical transition or phase shift; however, the term "regime shift" is most consistently used in the literature. Based on available evidence, we propose the hypothesis that Hawaiian waterbird extinctions in the Holocene were caused by ecological regime shifts, primarily driven by climate change and species introductions. Paleoecological evidence indicates a regime shift in dry to wet dominant forest vegetation immediately prior to and during the Polynesian era in some regions due to climate shifts or introduced predators. Regime shifts may have also been driven by trophic cascades, whereby a removal or change in abundance of species in one trophic level impacted species in higher or lower trophic levels (Folke et al., 2004, 2010). The decline in forest species may have caused an ecological cascade effect of secondary extinctions of herbivorous waterbirds during the Polynesian era. Indeed, a number of papers provide evidence that species extinctions in other regions were driven by shifts in climatic changes that caused shifts in vegetation regimes (Grayson, 1987; Ochoa & Piper, 2017) or species assemblages (Hunt, 2007; Owen-Smith, 1987; Villavicencio et al., 2015; Widga et al., 2017; Zimov et al., 1995).

CONCLUSIONS

In this review, we evaluated evidence from the existing literature on possible extinction times of Hawaiian waterbirds based on the time they were last observed in the fossil record. We then evaluated evidence for four proposed hypotheses for the drivers of waterbird extinctions in the Hawaiian Islands during the Holocene: (1) the overkill hypothesis; (2) the deforestation hypothesis; (3) the climate change hypothesis; and (4) the species introduction hypothesis. Of the 18 extinct waterbird species with subfossil evidence, 10 species were last observed in the fossil record prior to Polynesian arrival, and 6 species were last observed at the onset of or immediately following Polynesian arrival. We found a lack of evidence for the overkill and deforestation hypotheses and stronger evidence for the climate change and species introduction hypotheses. However, we contend that a suite of factors and their cascading effects—known as a regime shift—is the more likely cause of waterbird extinctions in the Hawaiian Islands. While fossil remains can help provide information about past species assemblages, the formation of fossils is a relatively rare event, particularly on tropical islands where the humid environment expedites decay of animal bones. Thus, caution should be taken when drawing conclusions about historical species extinctions, particularly those pertaining to human–wildlife interactions.

Here we have reviewed evidence relating to the historic causes of waterbird extinctions, but our proposed "regime shift extinctions" hypothesis may be applied to other avian taxonomic groups in the Hawaiian Islands and other systems, suggesting areas for further inquiry. We invite a reexamination of the evidence for causes of extinctions pre- and post-human arrival and highlight the need to acknowledge the influence of worldview on the process of scientific inquiry and interpretation of evidence, given impacts on conservation actions and policy today.

AUTHOR CONTRIBUTIONS

All authors assisted in the conception of the topic and framework of the paper. Kristen C. Harmon performed the literature reviews and wrote the first draft, including figures and tables. Melissa R. Price and Kawika B. Winter reviewed and authored drafts of the paper, figures, and tables.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Harmon et al., 2026) are available through the University of Hawai‘i's repository Scholarspace: https://hdl.handle.net/10125/111243.

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