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RESEARCH

Māori practitioner knowledge indicates a shift in forest fruit biomass and phenology over 75 years

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Abstract: Rapid alterations in plant and animal phenology driven by global climate change and rising temperatures can have far-reaching consequences for cultural and ecological systems. We documented changes, and mechanisms behind the changes, in fruit biomass and phenology in mixed podocarp-hardwood forests in the central North Island of New Zealand since the 1950s using the traditional knowledge (herein referred to as mātauranga) of Indigenous Māori (Tūhoe Tuawhenua and Ngāti Whare) forest practitioners. We also explored the likely cascading consequences of alterations in fruiting systems for forest frugivores, below-ground subsystems, local livelihoods, and language. Practitioners reported that the frequency of fruiting, crop size, and individual fruit size and quality declined significantly over the last 75 years, with the timing of fruit ripening often delayed by three months. A general warming trend, combined with less frequent and later frosts, and increased weather variability such as strong wind events, were identified as mechanisms that have impacted fruiting. Alterations in fruit biomass and phenology have also adversely impacted the body condition, breeding rates, and abundance of kererū | New Zealand pigeon (*Hemiphaga novaeseelandiae*) and feral pigs (*Sus scrofa*), two important food species for the community in the forest. Practitioner estimates of historic fruit inputs suggest that there were substantial nitrogen (N) returns to the below-ground subsystem from fruit that were 1–2 orders of magnitude higher than those reported from forest fruit fall elsewhere, and which are now severely reduced. The reduction in nutrient inputs and simple carbohydrates (e.g. sugars) in the fruit pulp to the soil is likely to have greatly impaired forest soil microbial activity, earthworm densities, and soil decomposition processes and rates, and ultimately the supply of soil nutrients for trees. Retention of mātauranga and nomenclature related to fruit are important for comprehension of past ecological states, and for future customary management goal setting and decision-making.

Keywords: climate change, frugivore, Indigenous peoples, nutrients, seedfall, traditional knowledge

Introduction

Global warming and increasing variability in extreme weather events have had far reaching and escalating effects on biodiversity, triggering cascading impacts on human livelihoods and wellbeing (Maxwell et al. 2019; Shivanna 2022; IPCC 2023). Altered climates can induce changes in vegetation that could transition some biological communities into alternate states from which recovery may be difficult (Beisner et al. 2003). Additionally, these shifts increase the vulnerability of ecosystems to additional pressures (e.g. impacts of invasive species) that could push them beyond a safe functioning threshold, resulting in a state of hysteresis (Rinawati et al. 2013).

Rising temperatures can cause temporal shifts in the seasonal calendar of species, including the reproductive phenology of flowering plants (Allen et al. 2013; Colautti et al. 2017; Pecl et al. 2017; Cohen et al. 2018; Piao et al. 2019; Stemkovski et al. 2022). Key aspects of flowering and fruiting phases include the frequency, timing, duration, intensity, and degree of synchrony among and within species (Rathcke & Lacey 1985; Newstrom et al. 1994). While rising temperatures are a key driver of change in the timing and magnitude of flowering and fruiting, local conditions such as nutrient resource availability, and extreme weather events such as droughts, heat waves, frosts, and heavy precipitation can also drive change (Diez et al. 2014; Maxwell et al. 2019; Weiskopf et al. 2020). Ongoing shifts in the reproduction of

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flowering plants can disrupt species interactions, triggering cascading effects on organisms that rely on these plants. While much of the research to date has focused on the impacts on mutualists such as pollinators and seed dispersers (e.g. Rafferty et al. 2015), shifts in phenology and reproductive biomass will have cascading consequences across ecosystems, including on below-ground processes (Zackrisson et al. 1999; Yang et al. 2008) and on cultural systems (Herman-Mercer et al. 2020).

Knowledge of the timing of plant reproductive phenological events (e.g. flowering, fruiting, and seeding) has been crucial for human survival, especially in agricultural and subsistence hunter-gatherer societies. Phenological events shape the connection of Indigenous cultures to place and time, and impact their foods, medicines, language, trade, ceremony, health, and wellbeing (Turner 1995; Thornton 1999; Bond et al. 2019; Herman-Mercer et al. 2020). For the Lun Bawang and Penan communities of Borneo, sightings of fruit ripening and fall predict seasonal weather cycles, the abundance and movement of Bornean bearded pigs (*Sus barbatus*) in forests, and timing of agronomic cultivation such as land preparation and seed sowing (Hosen et al. 2020). Plant phenology also frequently serves as an indicator for ecological events such as the arrival of other animal species and the optimal time to harvest plants and animals (see Peacock 1992; Lantz & Turner 2003; Turner & Reid 2022). For the Nuu-Chah-Nulth peoples of Vancouver Island, Canada, the ripening of salmonberries (*Rubus spectabilis*) was a signal for the return of adult chum salmon (*Oncorhynchus keta*) to rivers (Lantz & Turner 2003). Also, the flowering of red elderberry (*Sambucus racemosa*) heralded the appropriate time to fish for halibut (*Hippoglossus stenolepis*; Bouchard & Kennedy 1990). In Aotearoa | New Zealand (herein referred to as Aotearoa), fruit phenology in indigenous forests plays a crucial role in the timing of annual subsistence and cultural activities for many Māori communities. Forest fruits are still eaten and included as ingredients in different products (e.g. tawa fruit pulp and kernels used to make porridge, cakes, and bread), albeit less frequently than they were historically (Best 1942). Forest fruits are also important seasonal foods for native avian frugivores such as kererū | New Zealand pigeon (*Hemiphaga novaeseelandiae*), kākā (*Nestor meridionalis*), and kōkō/tūī (*Prosthemadera novaeseelandiae*), and likewise for non-native feral pigs (*Sus scrofa*); all of these species were seasonally harvested by Māori (Best 2005; Lyver et al. 2008; Carpenter et al. 2021). Declines in native bird populations (including of kererū, kākā, and kōkō) resulted in their harvest becoming prohibited under a complex history of colonial wildlife protection laws dating back to 1861 (Miskelly 2014). However, in some regions where these species were still abundant, covert community harvests continued into the 1950s to 1960s, with some smaller individual harvests occurring (Lyver et al. 2008).

Despite considerable annual temperature fluctuations over the past century (McGlone and Walker 2011), eight of the warmest years in Aotearoa between 1909 and 2022 occurred over the period 2012–2022 (Ministry for the Environment & Stats NZ 2023). The growing season in Aotearoa has lengthened and the number of frost days has decreased in most regions between 1972 and 2022 (Ministry for the Environment & Stats NZ 2023). Climate-induced warming is predicted to affect nearly every aspect of terrestrial ecosystem functioning in Aotearoa (McGlone & Walker 2011), including in forest ecosystems. Longitudinal studies of plant reproductive phenology, including seed rain datasets, are scarce in Aotearoa, which limits our knowledge and understanding of the response of phenology to past and future climate change. Flowering and fruiting phenologies in Aotearoa are broadly similar to those in many other temperate regions that have spring and summer flowering and autumn and winter fruiting (Ting et al. 2008; Richardson et al. 2023), but in coastal and lowland regions these seasonal patterns are attenuated by Aotearoa's highly maritime climate; flowering can occur throughout the year, species can have multiple flowering periods, and fruit ripening is often protracted over many weeks or months (Wardle 1978). Thus, changes in flowering and fruiting in response to climate change may be difficult to detect, especially in the context of highly variable oceanic climates (McGlone & Walker 2011). Indeed, over a decade since McGlone and Walker's (2011) initial predictions, direct evidence of climate change impacts on the reproductive phenology of Aotearoa trees is still rare (Keegan et al. 2022), especially for the compositionally complex forests that remain in Aotearoa's northern and lowland regions. While several studies have modelled potential impacts of climate change based on mast seeding mechanisms (e.g. Kelly et al. 2013; Monks et al. 2016), few studies have empirically demonstrated shifts in the frequency and abundance of seeding (but see Richardson et al. 2005; Allen et al. 2014; Yukich Clendon et al. 2023), and we are not aware of any studies that have examined how the timing of fruiting and flowering may have changed. This is because Aotearoa lacks longitudinal datasets on plant reproductive phenology that span more than a few years.

Disruption to phenological events and seasonal cycles is projected to increase as global warming and climate variability intensifies. Understanding the repercussions for ecosystem function both above- and below-ground will be important for forming and adapting Indigenous community decisions to protect resources and associated cultural identity, practices, and expression (Yang et al. 2008; IPCC 2023). The aims of this study therefore were to document changes in fruit production and reproductive phenology of native woody species in a mixed podocarp-hardwood forest (a dominant forest type in Aotearoa) observed by the Māori elders and practitioners (herein referred broadly to as practitioners) from Tuawhenua (a sub-group within the Tūhoe nation) and Ngāti Whare over the last 75 years. Through the oral accounts from practitioners, we developed a phenological calendar and collated te reo Māori (Māori language) terminology that captures the timing, condition, and biomass of fruiting events within this forest type. We recorded the mechanisms suggested by practitioners that they believed were driving shifts in fruit phenology, and synthesised this knowledge with respect to the cascading effect these shifts have had on the wider forest cultural-ecological system, including the condition and breeding of an avian frugivore (kererū) and omnivorous non-native ungulate (feral pig). Finally, we considered the consequences that these changes have had on the knowledge and language systems of Tuawhenua and Ngāti Whare.

Methods

Background and study location

We worked with Tuawhenua practitioners whose traditional territory includes a region within the heavily forested Te Urewera mountain ranges located in the North Island of Aotearoa (Fig. 1). In 2023, 51 039 people identified as Tūhoe in the national census, with more than 20% living on,

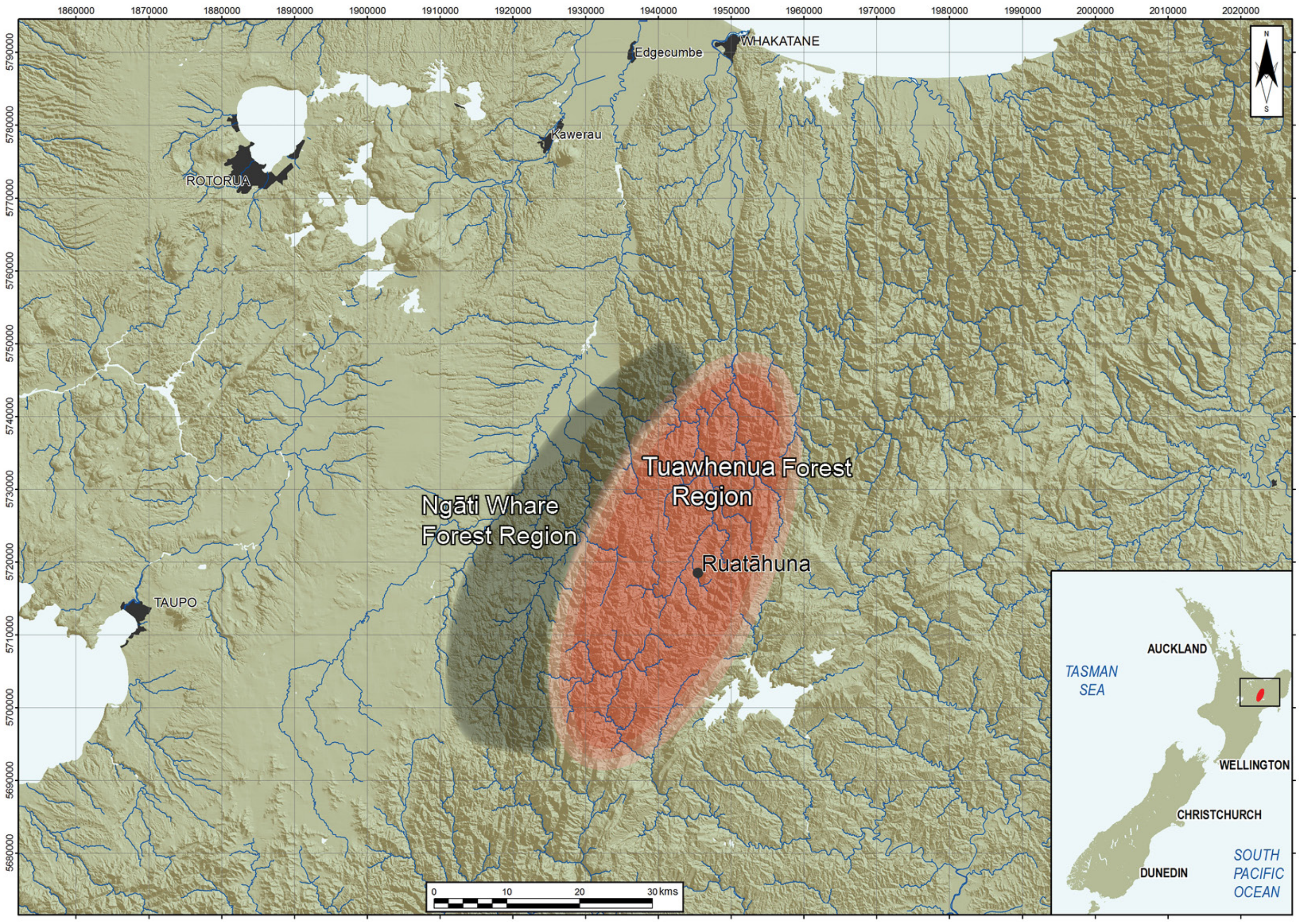

Figure 1. General locations of the Tuawhenua (part of Te Urewera) and Ngāti Whare (part of Whirinaki) forest regions of the central North Island, Aotearoa.

or in the immediate proximity of, their tribal lands (https://tewhata.io/tuhoe/social/people/demographics/, accessed 24 September 2025). The remainder largely live in towns surrounding Te Urewera and in major North Island cities. The Tuawhenua village of Ruatāhuna at the heart of Te Urewera has approximately 300 permanent residents clustered around ten marae (communal meeting places) established by eight different, but related, sub-tribes (Morunga & Tahi 2013). Ngāti Whare is a tribe of the central North Island, whose traditional territory encompasses Whirinaki Te Pua-a-Tāne Conservation Park. The tribe is represented through Te Rūnanga o Ngāti Whare, a common law trust established by the tribe in 1999. In 2018, the tribe numbered approximately 1533 members associated with two marae across eight associated sub-tribes (https://tewhata.io/ngati-whare/social/people/demographics/).

Ruatāhuna forest

Ruatāhuna is surrounded by c. 20 000 hectares of podocarp-hardwood forest (McKelvey 1973; Carswell et al. 2007) owned by Tuawhenua people. Tuawhenua lands typically rise steeply from c. 400 m a.s.l. in valley bottoms to c. 800 m a.s.l. on ridge crests. Forest canopies are dominated by evergreen angiosperms such as tawa (*Beilschmiedia tawa*), tawhero (*Pterophylla racemosa*), and rewarewa (*Knightia excelsa*), with emergent northern rātā (*Metrosideros robusta*) and conifers in the Podocarpaceae family such as rimu (*Dacrydium cupressinum*), toromiro (*Pectinopitys ferruginea*), matai (*Prumnopitys taxifolia*), kahikatea (*Dacrycarpus dacrydioides*), and tōtara (*Podocarpus totara*). These podocarp conifers are fleshy fruited and dioecious. Historical burning has generated large areas dominated by kānuka (*Kunzea ericoides*). About 30% of Tuawhenua forests were logged for conifers (> 30 m height, > 1 m stem diameter) by private forestry companies between 1950 and 1975, particularly the alluvial terraces and accessible toe-slopes. Post-logging regeneration of conifer species has been poor (Carswell et al. 2007; Wardle et al. 2008) and forests are now dominated by hardwood species such as tawa, tawhero, and hīnau (*Elaeocarpus dentatus*), and an abundance of subcanopy tree ferns (Carswell et al. 2007). For a list of Tūhoe Tuawhenua plant names and corresponding species of kererū food sources in the Tuawhenua region of Te Urewera, please refer to Appendix S1 in Supplementary Materials.

The rivers and forests around Ruatāhuna provide the community with a valued source of native and introduced plants and animals for food, traditional medicine (rongoā), building, clothing, weaving, carving materials, firewood, and cultural, recreational, and commercial activities. Recreational hunting (e.g. red deer [*Cervus elaphus*], rusa deer [*Rusa timorensis*], and feral pig) and commercial trapping (e.g. common brushtail possum [*Trichosurus vulpecula*]) of introduced mammal species provide valued sources of protein and fur, respectively.

Whirinaki Te Pua-a-Tāne Conservation Park

Whirinaki is a 55 000 ha forest area bordering the western boundary of the Ruatāhuna forest (Fig. 1). The area is principally within the tribal territory of Ngāti Whare, and includes the small, predominantly Māori settlements of Te Whāiti and Minginui. Ngāti Whare and the Department of Conservation jointly manage the park (Department of Conservation 2017). Much of the park remains in forest, consisting of rimu, matai, tōtara, toromiro, and kahikatea as emergents over a canopy of tawa, tawhero, and rewarewa, with a subcanopy of māhoe (*Melicytus ramiflorus*) (Morton et al. 1984; Smale et al. 1987; Powlesland et al. 2003). Accessible terrace forests in Whirinaki were logged up until 1984, but small protected areas retained dense stands of tall podocarp conifers (Beveridge et al. 2004).

Knowledge collection and transcription

Five rounds of interviews and four knowledge verification workshops were conducted with Tuawhenua and Ngāti Whare forest practitioners between 2004 and 2018 (Table 1). Purposive and snowball sampling approaches were used to recruit practitioners for interview, whereby recommendations of other subject matter experts were made by practitioners from both regions (Guest et al. 2006; Cohen & Arieli 2011). Forest practitioners were selected based on their knowledge of the forests stemming from their current or past use and experience with the forest. All participants were either originally from the Te Urewera or Whirinaki regions or had lived within these communities for over 35 years. Individuals were identified and approached for interview by two researchers with genealogical ties to Tuawhenua and Ngāti Whare, who had knowledge of who the subject matter experts were in the community.

Interviews were conducted by five Māori researchers, of whom four were from the local communities, to ensure that participants felt comfortable and that the process was conducted within a culturally safe and appropriate environment. We took a semi-structured approach to the interviews and initially used open-ended questions to allow for more natural conversation to occur with practitioners and unanticipated insights to emerge (Huntington 2000; Telfer & Garde 2006). However, as themes progressively began to emerge through the different rounds of interviews, questions became more directed in later interviews, especially if a practitioner had been interviewed in earlier rounds. Interviews were conducted in both the Māori and English languages, depending on the preferences of the participants, and audio recorded. At the time of the interview each interviewee was given the list of questions written in both Te Reo Māori (Māori language) and English so they could follow the questions as they were asked. Those interviews that were conducted in Māori were transcribed and translated into English, with the translations verified by local practitioners fluent in Māori and the local dialect to ensure accuracy and cultural integrity. Interviews ranged from 45 minutes to 3 hours in length.

Interviews and theme development and verification

In the initial three sets of interviews, Tuawhenua practitioners were asked to broadly discuss the nature of their relationship, movements, customary practices, use of resources, and livelihood experiences within the Te Urewera forest system. The inquiry in the first set of interviews was focused predominantly around the kererū and its relationship with the forest fruiting and communities. These interviews gave the researchers a broad understanding of how the practitioners interacted with, used, and experienced the forests and natural resources.

A thematic analysis approach was then applied to derive recurring ideas and themes relating to forest fruiting and associations between fruiting and kererū (Braun & Clarke 2006). Based on the first three sets of interviews (Table 1), the initial phase of coding was conducted inductively using an open process to assemble broad domains relating to fruiting (Saldana 2016; Williams & Moser 2019). Following this process, a knowledge verification workshop (Table 1) was conducted with Tuawhenua practitioners to confirm the initial categorisation of domains, and to offer an opportunity to further discuss and provide additional information related to these domains. A fourth set of interviews was conducted with Ngāti Whare practitioners, again to broadly understand the nature of their relationship, interaction, and experiences with the Whirinaki forest system. Narrative was coded according to the thematic domains identified, and new domains were identified. A second knowledge verification workshop was conducted to provide confirmation of the domains and another opportunity to contribute information (Table 1).

Using the narrative from the four sets of interviews, a second cycle of coding was conducted to derive the main themes, which included (1) changes in fruit biomass and condition, (2) changes in the phenology of fruiting, (3) changes in fruit biomass and phenology as related to kererū abundance, condition, and foraging behaviour, (4) explanations and mechanisms for changes in fruit abundance and phenology, (5) local indicators of fruiting abundance, size, and condition, and (6) Tuawhenua and Ngāti Whare nomenclature related to fruiting abundance and condition.

Based on these themes, a fifth set of interviews (Table 1) was conducted with practitioners to provide confirmation around the emergent themes, but in particular to verify and cross-check (1) forest fruiting indicators, (2) the gradients of how practitioners understood fruit abundance, size, and quality, (3) the size and quality of fruit in the canopy and on the ground in Te Urewera and Whirinaki forests, and (4) the terminology to describe those states. A third verification workshop (Table 1) was conducted with practitioners to further explore practitioner knowledge of indicators and language. It is important to note that during this process meetings with some practitioners were conducted individually or in pairs at their homes to cross-check and verify information they provided.

A final three-day marae-based and on-the-land workshop was conducted with the community so that practitioners could present and discuss knowledge relating to fruiting indicators and dynamics, and in particular to how fruiting was associated with the kererū (Table 1). We used this opportunity to finalise and verify our information. We also used it to probe deeper into their observations and understanding of the themes identified, indicators relating to historic baselines of fruiting events and patterns, and their explanations for mechanisms they thought were impacting fruiting. Where practitioners indicated a relationship with the kererū, we focused our enquiry on how the bird's abundance, condition, and foraging behaviour were linked to forest fruiting seasonality and biomass. Knowledge of past timber extraction and changes in weather events and patterns in the region were also recorded.

Table 1: Number, gender, and age of Tuawhenua and Ngāti Whare practitioners that contributed to interviews and knowledge verification workshops relating to changes in fruiting biomass and phenology and associated kererū behaviour. Interviews and workshops were conducted between 2004 and 2018 (note: some practitioners contributed to more than one knowledge collection and verification stage).

Knowledge collection and verification stages	No. of male practitioners	No. of female practitioners	Age class 16–40 years	Age class 41–60 years	Age class 61–80 years	Age class 81+ years	Total practitioners
Interview 1: Mātauranga o te kererū (Tuawhenua, 2004–2006)	10	0	0	6	2	2	10
Interview 2: Mātauranga o te Tuawhenua (Tuawhenua, 2006–2012)	20	7	0	5	20	2	27
Interview 3: Mātauranga o te taiao (Tuawhenua, 2014)	29	14	9	12	21	1	43
Workshop 1: Identification and verification of changes in state and timing of fruiting (2015)	7	6	–	8	5	–	13
Interview 4: Mātauranga o te taiao (Ngāti Whare, 2016)	7	3	–	1	8	–	9
Workshop 2: Identification and verification of reasons for changes in state and timing of fruiting (2016)	4	5	–	1	8	–	9
Interview 5: Mātauranga tohu taiao (Tuawhenua, 2017–2018)	32	11	8	12	22	1	43
Workshop 3: Confirmation and verification of fruiting indicators and terminology (2017)	4	6	–	–	9	1	10
Workshop 4: Confirmation and transfer of knowledge relating to kererū and associated fruiting dynamics by practitioners (2018)	21	18	4	7	26	2	39

Results

Changes in fruit productivity and biomass

Tuawhenua and Ngāti Whare practitioners observed a significant decline in fruit abundance and the frequency of fruiting events across a variety of species in both the Te Urewera and Whirinaki forests over the last 30 years, even in the more remote blocks (Tables 2 & 3). In particular, it was reported that there was much less tawa fruit in the forest. It was reported that, prior to the 1990s, it was possible to flick a couple of leaves and you would find tawa fruit. The decline in fruit abundance and frequency of fruiting has also been accompanied by a reduction in the size and condition of the fruit produced, noticeably in tawa and hīnau (Tables 2 & 3). Practitioners recounted that between the 1940s and late 1960s, tawa fruit were longer than a thumb of an average adult male (c. 6 cm long) and about the size of a small oval plum. However, tawa fruit started declining in size (and abundance) in the late 1960s and they are now approximately half the length (c. 2.5 cm long) they used to be (Table 3).

Practitioners noted that some trees would bear fruit even when it was not a good fruiting year overall. Even so, one practitioner reported that a grove of 25–50 toromiro trees growing on a face across from where he lived had not fruited in the past six years. This was highly unusual, as he noted that previously those trees would fruit annually, albeit with differing crop sizes depending on the year. Some plant species important for kererū had also declined extensively in occurrence. Before timber milling in Ngāputahi (c. 1940s and early 1950s), one of the practitioners recounted that all the streams were full of makomako (*Aristotelia serrata*), where it grew as thickets. He and his siblings would consume makomako leaves and the ripe fruit when in season. The practitioner described how their mouths would be purple from eating makomako fruit. However, this shrub seldom grows as a thicket now, but rather is observed as solitary plants or small isolated patches (Table 2).

Changes in fruiting phenology (in relation to the kererū)

Practitioners identified key tree species that followed a general ripening cycle, and whose fruit played important roles in the diet of kererū and other species, and more broadly in ecosystem functioning (Table 2, Fig. 2). Many of the early fruiting trees, i.e. those at the commencement phase of the fruiting calendar, were angiosperm species such as tawa, kōtukutuku (*Fuchsia excorticata*), makomako, kaikōmako (*Pennantia corymbosa*), kaiwēta (*Carpodetus serratus*), kāramuramu (*Coprosma robusta*), and tāwiniwini (*Gaultheria antipoda*) (Table 2). Ripe fruits of these species between December and March were important because they sustained kererū during early summer when other food sources were scarce. Practitioners knew that when fruits of these species started ripening, kererū would begin their breeding activities and display flights. Practitioners reported that it has, however, become increasingly common that fruit ripening by these species in the commencement phase is being delayed by up two months (Fig. 2).

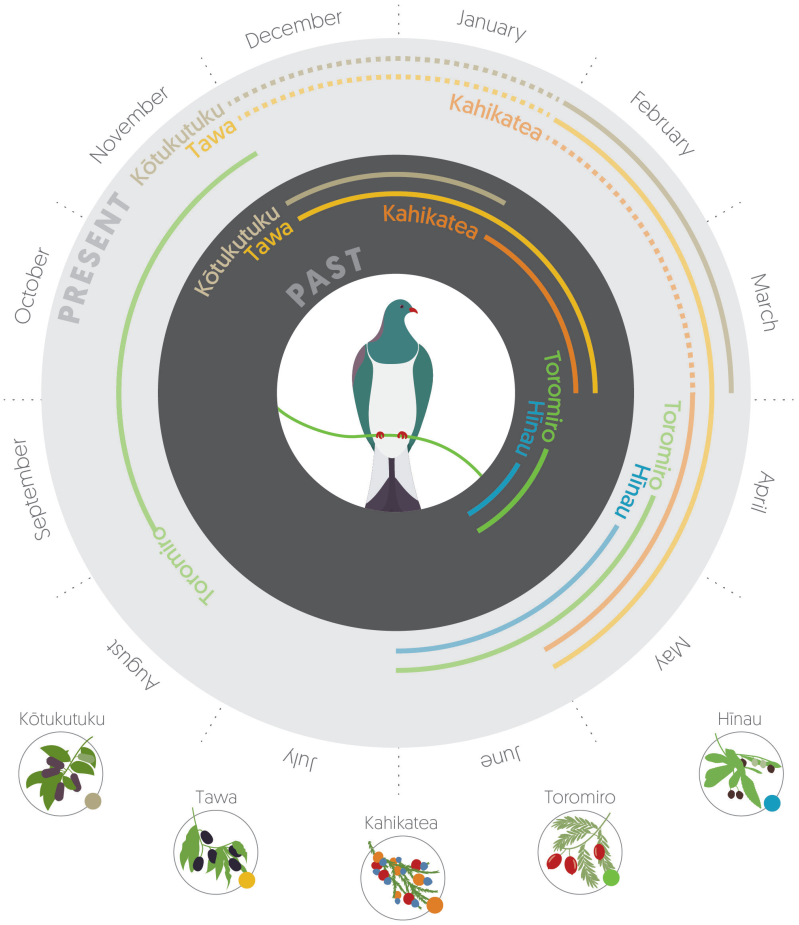

Figure 2. Temporal shifts in the phenology of fruit ripening in Tuawhenua (part of Te Urewera) and Ngāti Whare (part of Whirinaki) forest regions of the central North Island, Aotearoa. The dark grey annulus inner circle represents the historic timing (i.e. past) of fruit ripening for the five key species (kōtukutuku [*Fuchsia excorticata*]; tawa [*Beilschmiedia tawa*]; kahikatea [*Dacrycarpus dacrydioides*]; toromiro [*Pectinopitys ferruginea*]; hīnau [*Elaeocarpus dentatus*]) whereas the light grey annulus outer circle represents the timing observed by practitioners in contemporary times (i.e. present). The dashed arcs indicate that in some seasons the start of the ripening period of kōtukutuku, tawa, and kahikatea fruit still occurs as it did in the past.

Table 2: Order of fruiting phases and practitioner observations relating to the fruiting of trees dominant in the diet of kererū | New Zealand pigeon (*Hemiphaga novaeseelandiae*), in Te Urewera and Whirinaki forests, eastern North Island, Aotearoa.

Species	Fruiting phase	Usual months of fruit ripening	Phenological calendar and changes in fruit
Kōtukutuku (*Fuchsia excorticata*[1], Onagraceae)	Commencement	December–January	Ripening of kōtukutuku fruit can be delayed by two months
Makomako (*Aristotelia serrata*[1], Elaeocarpaceae)	Commencement	December–January	In the 1940s, makomako filled the gullies, but it has since died off Usually finished fruiting by January, but now can be two months later
Tawa (*Beilschmiedia tawa*)	Commencement	December–March	Tawa commonly bears fruit from December with peak ripening in January and February Tawa fruit were a main part of our food source and generally ready [ripe] from January through to March Tawa recently observed producing fruit twice during the year Up until the 1980s, heavy tawa fruiting was still occurring Up until the 1980s, the ground was still covered with tawa fruit, but now fruit are scattered amongst the leaf litter Tawa fruit started declining in size (and abundance) in the late 1960s Kernels inside of tawa fruit have shrunk over the last two decades Tawa fruit are now half the size that they used to be Tawa fruit are now black and scabby and about the size of a dried prune (c. 2.5 cm long) Often now the tawa fruit have rotted near the stem Tawa fruit on ground now rots much quicker compared with in the past For almost a decade or more there has been no tawa fruit There was a set time when tawa fruit would fall off the branches, but now you go to these places and cannot find many tawa fruit at all People would often skid and slip over on the crushed fruit when walking in the forest, but not anymore. Now there is nothing
Kaikōmako (*Pennantia corymbosa*[1])	Commencement	January–March	Usually finished fruiting by March, but now can be two months later
Kaiwēta (*Carpodetus serratus*[1])	Commencement	January–March	Usually finished fruiting by March, but now can be two months later
Tāwiniwini (*Gaultheria antipoda*)	Commencement	January–March	Historically the tāwiniwini grew in great abundance but less so now Usually finished fruiting by March, but now can be two months later
Kāramuramu (*Coprosma robusta*[1])	Commencement	January–April	Usually finished fruiting by end of April but can be now in June Fruiting usually occurs towards end of April, but now carries on into June
Horopito (*Pseudowintera colorata*)	Commencement	January–April	Kererū (and other avian frugivores) would flock to horopito groves particularly during April to feed on fruit in trees over three metres, but less so now
Kahikatea (*Dacrycarpus dacrydioides*[1])	Lead-up	February–March	Kahikatea fruit are ripening later in the year than normal Fruit usually ripen to red, orange, or yellow colours early in the year, but now they can still be green in March Fruit usually should have been gone by March, but some years now, it is just beginning to ripen in mid-April

Table 2: Continued.

Species	Fruiting phase	Usual months of fruit ripening	Phenological calendar and changes in fruit
Rimu (*Dacrydium cupressinum*[1])	Lead-up	February–April	Crop size of rimu fruit has declined over time
Matai (*Prumnopitys taxifolia*[1])	Lead-up	February–April	Matai fruit would be as plump and sweet as prized blue berries Matai fruit are now half the size and shrivelled like small raisins
Tōtara (*Podocarpus laetus*[1] and *Podocarpus totara*[1])	Lead-up	February–March	Crop size of tōtara fruit has declined over time
Toromiro (*Pectinopitys ferruginea*[1])	Peak	April–June	May and June are generally the peak months for toromiro fruit, however in some years fruiting may extend into July Under the best conditions (cold and calm) toromiro fruit from the beginning of April through to July, or even mid-August By the rising of Matariki (Pleiades) between mid-June to early July, the toromiro fruiting is usually complete During peak periods and towards the end of fruiting season toromiro fruit carpet the ground Heavy frosts ripen and set the fruit for longer periods if there are no severe storms or strong winds Recently, ripe toromiro fruit have been observed on trees from September to December Recently, there have been years when it was expected that toromiro should have already fallen but it had not yet ripened Toromiro observed with green fruit in July. The fruit did not ripen until November Toromiro fruit on the ground in September and October: this is not the right time of the year for those trees to be doing that Toromiro trees are producing fruit twice during the year Toromiro were observed with ripe fruit in November 2005 In 2016, it took a harvester 20−30 minutes to fill a bread bag full of toromiro fruit; harvesters were required to move around under the trees to collect the fruit. In the past it took 5 minutes to fill a bag in a heavy fruiting season A grove of 25−50 toromiro trees have not fruited in the past six years
Hīnau (*Elaeocarpus dentatus*)	Peak	May–June	Historically, fruit would blanket the canopy of hīnau trees, but this has declined over the years The frequency of heavy hīnau fruiting seasons has declined Hīnau fruit are not as abundant as they were, nor the size they used to be, in the 1950–1960s Historically, hīnau fruit would carpet the ground beneath the trees, but not now Historically, hīnau fruit were bigger than marbles, but have shrunk in size over the years Hīnau trees have been recently observed fruiting twice a year
Patatē (*Schefflera digitata*[1])	Finishing	June–July	These final fruit enable the kererū to retain their condition through winter When kereru feed on patatē fruit, their flesh takes on the flavour of that species

Table 2: Continued.

Species	Fruiting phase	Usual months of fruit ripening	Phenological calendar and changes in fruit
Pirita (*Ripogonum scandens*)	Finishing	June–August	These final fruit enable the kererū to retain their condition through winter When kererū feed on pirita fruit, their flesh takes on the flavour of that species

[1] dioecious or gynodioecious

Table 3. Tuawhenua and Ngāti Whare practitioner descriptions of fruit abundance, size, and quality in the forest canopy and on the forest floor in Te Urewera and Whirinaki.

Fruiting indicators	Fruiting gradient	Fruiting descriptors	Māori language fruiting nomenclature
Canopy	Heavy	Top canopy (kōmata) tree species has an intense colouration of yellow, orange, or red fruit (e.g. toromiro, kahikatea, rimu) or purple-black fruit (e.g. tawa, matai, tōtara, hīnau) Mid-canopy (poka) tree species have an intense red-orange (kāramuramu, tātarāmoa, tātarakehu, pirita) or purple-black (e.g. makomako, kōtukutuku, tāwiniwini, parapara, horopito, patatē) colouration of fruit Canopy has an appearance of being totally covered with fruit growing on top of each other Fruit bunched like grapes (e.g. makomako) – a handful of fruit easily peeled off Canopy totally covered with fruit so that it is difficult to see the leaves Trees in the forest canopy (with 50–75% fruit coverage) would be glowing orange-red when viewed from 500–2000 m away In groves of kahikatea, around eight out of 15 trees would be glowing orange It was not uncommon for tawa trees to be loaded with fruit yearly Tawa fruit would be bunched in the canopy, almost like grapes The canopy would be dark purple with fruit. When the tawa fruited heavily you could not see the leaves Approximately 70−100% of the canopy would be covered with tawa fruit Kāramuramu fruit used to bunch like grapes, with over 50% of the canopy bright orange In a heavy fruiting, the toromiro canopy would be intense red with fruit bunched like grapes. In a grove of 60−100 toromiro trees you could hardly see the trees for the kererū When the toromiro were ripe they looked like heavily laden grapes	Hāwere: Refers to a heavy fruiting season Pūwhero: Refers to 75% coverage of fruit across the top canopy (e.g. toromiro, kahikatea, rimū) and mid-canopy (e.g. tātarāmoa) Kōuriuri: Kahikatea canopy glowing an intense orange-red Mātotoru: Refers to the thick and extensive coverage of fruit Matomato ana: Refers to the rich and luscious colouration of leaves and fruit of a tree or grove Wherowhero ana: Refers to the intense red-orange colour of toromiro and kahikatea canopies in heavy fruit Tautau: Refers to branches straining and sagging with the weight of fruit Makuru ana: Refers to the proliferation and succulence of fruit Kōtawa or pokerehū: Refers to the fruit of the tawa Pōkere: Refers to the inner kernel of the tawa
Canopy	Moderate	Fruit spread-out and patchy Canopy partially covered with fruit and patchy but still has red-orange hue and a reasonable intensity of colour No grape-like bunching of fruit Less than half the trees in a grove in full fruit	He nanakia: Refers to some fruit but not a lot
Canopy	Poor	Canopy is just green with all the leaves exposed Fruit might be present but green from delayed ripening Trees fruit poorly but twice in a year	Koretake: Refers to a poor fruiting Ruha: Refers to the fruit and tree appearing old, without life or energy. Tauwhīroki: Refers to a lean fruiting season

Table 3. Continued.

Fruiting indicators	Fruiting gradient	Fruiting descriptors	Māori language fruiting nomenclature
Ground	Heavy	There used to be a 2.5−5 cm thick layer of kāramuramu fruit on the ground beneath trees In good years, there can be 2.5−5 cm layer of kahikatea fruit covering the ground beneath trees Tawa fruit used to be thick on the ground. Historically there could be a layer of tawa fruit beneath trees that was 5−10 cm thick It was not possible to see the forest leaf litter for the tawa fruit. This would be called a hapua tawa Historically (between the 1940s and late 1960s) the tawa fruit were huge: longer than your thumb (c. 6 cm long) and shaped like a small oval plum Tawa fruit used to measure from the middle knuckle to the end of the finger of an adult male The fruit would make a crunching sound underfoot. It was slushy and slippery to walk on because of the crushed fruit covering the slopes Consumption of five tawa fruit would be enough to give you a purple mouth Historically, an adult could scoop up a handful of tawa fruit off the ground with ease (hand overflowing) A single continuous layering of fruit across the ground Ground feels like carpet or mat and very soft underfoot Could collect a good meal of fruit off the ground with ease: someone could obtain a full handful of tawa and hīnau with one scoop In good years there can be a 2.5−5 cm thick layer of toromiro fruit covering the ground beneath trees An adult could fill a bread bag full of toromiro fruit in 5 minutes Observers cannot see the ground because it is totally covered with toromiro or hīnau fruit In good years there can be a double layering of hīnau fruit 5–7.5 cm thick across the ground beneath a tree Hīnau fruit used to be so abundant they would be collected and roasted on coal ranges or pounded to make flour for bread Very little pig rooting in the 1950s because the pigs were eating the abundance of hīnau and tawa fruit on the forest floor In a good fruiting season feral pigs are fat like a kunekune (a breed of pig bred for its fat to preserve foods) Feral pigs get so fat eating hīnau that pig hunters deliberately hunted areas near or beneath hīnau groves. Hunters could hear the cracking and crunching noise pigs made whilst eating the hīnau fruit from 100 m away Feral pig dung made up entirely of hīnau all over the place (a pile of pig dung every 5–10 m) In a good fruiting season hunters could observe the marks where feral pigs had dragged their stomachs through the mud Hunters had to pull feral pigs out of the forest with their horses because they were so big Feral pigs were plentiful and huge when forest fruit were regularly in abundance each year	Papahoro: Refers to where the ground cannot be seen because it is carpeted with fruit. Nothing of the ground is visible because its covered with fruit Horo: Refers to when toromiro are deep red and carpet the ground, usually at the end of fruiting season or directly after a severe storm Māhora ana: Refers to fruit being laid out like a mat or carpet across the ground Kōputu hīnau: Refers to an extensive heaping and covering of hīnau fruit across the ground
Ground	Moderate	Less than a finger spacing between fruit on the ground While walking in the forest you could easily stand on five fruit or more with each step Fruit is scattered with one to three fruit within a hand spacing Fruit laid out like a mat Only able to scoop up a part-handful of fruit Fruit is scattered covering approximately half (50%) of the visible ground	

Table 3. Continued.

Fruiting indicators	Fruiting gradient	Fruiting descriptors	Māori language fruiting nomenclature
Ground	Poor	The ground in the forest feels hard under foot Fruit are sparse and scattered across the forest floor beneath trees Individual fruit scattered across the ground can be 30–90 cm apart, requiring fruit to be picked up rather than scooped up Only about 10% of the forest floor is covered by fruit under the drop-line Feels like a chore to put fruit into piles: it's hard work You get a sore back from bending over to collect fruit off the ground because they are so spread out Feral pigs are skinny from the lack of fruit in their diet Feral pigs and their meat now have a mud aroma from having to root out the large earthworms, as well as pikopiko and mauku[1], from the forest floor	
Quality	Good size and condition	Fruit described as large, plump, and sweet The fruit is juicy and ripens on the tree The fruit keeps much longer on the tree and can be found in the following season	Makuru: Refers to fruit that is large, plump, and sweet in taste Pure: Refers to new food or the first fruits which emerge in early December
Quality	Poor size and condition	Fruit has generally become smaller and drier Fruit also tastes bitter now Fruit fail to ripen on the tree but they have fallen to the ground Fruit is green and going rotten without reaching its maturity A lot of the fruit has rotted near the stem now. The fruit is not perfect like it used to be Fruit appear to have a type of blight affecting them Size of fruit prior to the 1970s substantially larger than they are now [in 2017]	

[1] *Asplenium bulbiferum*

The second phase involved fruit ripening by species such as kahikatea, matai, rimu, and tōtara in the lead-up phase, which extended from late summer into autumn (Table 2, Fig. 2). These species supported kererū to feed their young, but also with nourishment to build up reserves for the peak period of foraging. Practitioners reported that when they observed the kahikatea in full fruit, they would know that the rimu and the tōtara would be not far behind. If these lead-up species did not fruit well, then practitioners expected that it would also be a poorer season for the hīnau and toromiro in that year.

Practitioners reported that while the tawa and hīnau would fatten kererū, it was the toromiro that made the birds extremely fat. They recognised that the peak ripening of toromiro and hīnau fruit in May and June was a critical period as it allowed the birds to build fat reserves for their survival through the winter. However, it was observed that toromiro could begin fruiting as early as late April, and could persist on the trees into July, if there were heavy frosts whilst the fruit was ripening. Without the heavy frosts during ripening, the fruit would fall early or not ripen at all. As the toromiro and hīnau fruiting eased and before kererū transitioned to foraging on leaves, they would shift their diet to include fruits from the finishing phase such as the pirita (*Ripogonum scandens*) and patatē (*Schefflera digitata*), which began to ripen between June and August (Table 2). By foraging on these final fruits, kererū retained their condition before shifting to browse foliage in the austral spring.

Several practitioners observed an increasing variability in the timing of fruiting within the forest, with one describing the phenomenon as “some of the trees in the forest no longer knowing if it is winter or summer or which season of the year it is”. Traditionally, it was widely recognised that there would be very little fruit available on the trees between August and December. Over the last two decades however, practitioners have noted a shift, with fruiting and ripening now occurring later in the year, disrupting the natural seasonal rhythms (Fig. 2). One striking example reported by practitioners was the unusual ripening of toromiro in September, October, and even November, a period during which fruiting was historically unheard of for this species. Additionally, they noted instances where fruit remained green during periods when it was traditionally expected to be ripe. This disruption also extends to flowering, with reports of trees flowering later in the year or even during the winter months—an uncommon occurrence in the past. Conversely, practitioners have observed cases where fruit ripened earlier than expected, leaving trees bare by the time they would typically reach full ripeness. In some instances, there have even been reports of double fruiting periods within the same year, a highly unusual phenomenon that further underscores the increased unpredictability of fruiting cycles.

Suggested mechanisms for shifts in fruiting phenology

Practitioners reported that summer was being “drawn out” and that since the 1990s there has been a distinct lack of frosts in March and April, which meant that fruit did not set or ripen appropriately, causing it to fall earlier and more quickly. They also linked the warming and increased variability in the weather to lower fruit production. Practitioners recognised that fruit would not persist as long on trees during a mild autumn or winter. They had also observed more frequent strong wind events which caused premature fruit fall.

Increased drying and a decline in moisture held within the forest was reported by some practitioners. It was observed that all the small streams of the main range were drying up. Streams where the practitioners historically caught tuna | New Zealand longfin eel (*Anguilla dieffenbachii*) had significantly reduced flows and the tuna were gone. Drying within the forest was attributed to a warming climate, but was thought to have been exacerbated by the removal via logging of large podocarp trees, and a subsequent predominance of hardwoods; drying out was also attributed to heavy browsing by introduced ungulates, e.g. red deer, cattle (*Bos taurus*), horses (*Equus caballus*), which remove understorey vegetation and open up the forest, exposing the soil. Practitioners recognised that historically the trees and understorey vegetation would have held a lot of moisture and released it slowly. As such, water was no longer continually percolating into the aquifers and supporting a regular flow in the streams. The hardening of the ground also meant that rainfall was more inclined to run off over the surface. As such, the increased intensity and frequency of rainfall events, and associated run-off, had eroded and gouged out creek-beds to an extent that they looked more like drains.

Impact of changes in fruiting biomass and phenology on kererū and feral pigs

From the late 1970s onwards practitioners reported observing a change in the condition of the kererū, which they linked to changes in fruit biomass and phenology. It was common between 1950 and 1970 for kererū to hit the ground and burst open after being shot because they were so excessively fat. However, since the 1970s, hunters observed that kererū no longer attained this excessive fatness and were more frequently in poorer condition, to a point where they ceased to hunt them. Initially, this decline in condition was attributed to poor individual fruiting seasons, but the abundance of kererū also started to dramatically decline. Practitioners then recognised that declines in fruit abundance (including loss of fruit to strong wind events) and the increased irregularity (i.e. delays) in fruit growth and ripening had disrupted the foraging behaviour of the kererū. It was reported that warming temperatures were also linked to a failure of fruit to adequately ripen in some years, making it less palatable for birds like the kererū; however over the last decade the birds had been observed eating unripe fruit.

Practitioners suggested that the lack of food in the forest was the reason kererū were increasingly dispersing beyond the forest to forage for other food sources. Increasingly, kererū had been observed by practitioners leaving the cover of the forest to cross open ground to feed on the flowers, new shoots, and leaves of non-native willows (*Salix* spp.), tree lucerne (*Cytisus proliferus*), and the fruit of domesticated fruit trees (e.g. plums [*Prunus* × *domestica*] and cherries [*Prunus avium*]) around where humans live. Recently, one practitioner observed 25 to 30 kererū feeding on the fruit in plum trees adjacent to their home, so could only assume that food was lacking in the forests. It appeared to practitioners that kererū no longer settled for long to feed as they were disrupted and continually moving around. Practitioners also reported that the irregularity in fruiting meant that kererū were not eating fruit at the appropriate times, even when there was fruit on the trees, and were hungry. It was suggested that the trees have changed their phenology, but that the kererū had yet to adjust.

Practitioners reported that changes in fruiting phenology had influenced an important non-native food species for communities, the feral pig. One of the oldest practitioners reported that during the 1940–1950s, feral pigs seldom excavated the ground for food owing to the volume of food, in particular, the hyperabundance of fruit, on the forest floor. Another practitioner recalled accounts from his elders where they had observed smooth drag marks through the mud, caused by the extended stomachs of well-conditioned pigs as they walked through the mud. The tawa, and particularly the hīnau, were reported to be important fruit species for the pigs. Tawa fruit were known to keep the pigs sated until the hīnau fruited. Practitioners noted that in years when there were carpets of hinau fruit covering the forest floor there would be a noticeable increase in feral pig numbers over the next 6–12 months. The reduction in fruit biomass throughout the forests meant the removal of a major food item for feral pigs. This had changed the foraging behaviour of the pigs and they had increasingly started excavating the forest floor to locate food. It was observed that pigs seldom reach the numbers or condition now that they did historically.

Discussion

Loss of fruit biomass from hardwood-podocarp forest in Aotearoa | New Zealand

Practitioners in this study linked delayed ripening, lower production, reduced size, and poorer quality of fruit of key tree species in Te Urewera and Whirinaki over the last 30−40 years to a general warming and the delayed and reduced frequency of frost events during autumn. Whilst frosts can cause blistering or bursting of fruit in orchards and vineyards, practitioners reported that these cold events were crucial to priming the condition and persistence of fruit during the lead-up and peak fruiting periods. Despite some regional variability, the frequency of frosts decreased across Aotearoa over the period 1972–2022 (Clark and Sturman 2009; Stats NZ 2023). Life cycle stages of plants, such as the timing of flowering, budding, and fruiting are influenced by a complex combination of climatic and non-climatic factors and events (Nagy et al. 2013; Butt et al. 2015) which can have longer term flow-on effects to vertebrate and invertebrate fauna (Maron et al. 2015; Renner et al. 2018). Although temperature is often considered a primary driver of changes in plant reproductive phenology, local conditions such as resource availability, frost, and precipitation events are also important (Jentsch et al. 2009; Diez et al. 2014).

Aotearoa has a warm temperate climate in its north and a cool or cold temperate climate to the south, with broadly equable monthly rainfall across the year, and native forests covering almost a quarter of the landscape. Whilst some native tree species, such as tōtara, have shown some level of resilience to habitat changes and warmer temperatures (McGlone & Walker, 2011; Ryan 2017), many tree species have shallow rooting systems and weak stomatal control, and hence are only weakly adapted to drought (Laughlin et al. 2020). More frequent dry spells may slow growth rates and diminish competitiveness, or even directly kill some individuals. Studies from mast seeding tree species suggest that trees are primed to flower and fruit following mild, wet summers during which plants accumulate carbon resources through high net photosynthesis, and nutrients through high mineralisation rates in the soil (Richardson et al. 2005; Smaill et al. 2011; Allen et al. 2018). We suggest that without these periods of high resource availability, fruit production may decline.

Consequences of changes in fruit biomass and phenology for avian frugivores

Kererū populations have undergone order of magnitude declines in the Tuawhenua and Whirinaki forests and across Aotearoa over the last century (Pierce et al. 1993; Higgins et al. 2001; Carpenter et al. 2021). Large seasonal flocks of ≥ 700 birds that were observed historically are now non-existent (Lyver et al. 2008). While predation of the eggs, chicks, and adult kererū by introduced mammalian predators is a significant contributor to the decline in kererū (Carpenter et al. 2021), historical logging of rimu, kahikatea, matai, and toromiro, combined with fruit being eaten by non-native animals (brushtail possum and ship rat [*Rattus rattus*]; see Carpenter et al. 2025) were also recognised as having a significant impact on kererū. We predict therefore that if current kererū populations were to be released from predation limitations, the magnitude of fruit biomass loss and increased variability in the ripening of fruit that has been occurring in the Tuawhenua and Whirinaki forests would have significant consequences for the breeding and survival of kererū.

Fruit of native trees contributes a large proportion of the kererū diet in the Tuawhenua and Whirinaki forests (Powlesland et al. 2003; Emeny et al. 2009) as well as more generally throughout Aotearoa (Campbell et al. 2009). However, despite having a high carbohydrate content, fruit pulp is considered nutritionally inadequate for frugivorous birds because of its low protein content (Bosque & Pacheco 2000). It is also recognised that in kererū, the dietary switch from fruit to the foliage of tree species such as mahoē and kōwhai in winter provides a relatively better source of protein and nutrients (Emeny et al. 2009). However, practitioners in this study emphasised that the seasonal role of fruits like toromiro and hīnau contributed to the kererū developing a seasonally high body mass index that bolsters its over-winter survival and breeding in spring. This aligns with evidence from the Chatham Islands, Aotearoa, where heavy fruiting of Chatham Island matipo (*Myrsine chathamica*) and hoho (*Pseudopanax chathamicus*) promoted early and prolonged nesting of the parea (*Hemiphaga chathamensis*), a close relative of the kererū (Powlesland et al. 1997).

Based on recent practitioner observations of kererū increasingly foraging on the flowers, fresh shoots, leaves, and fruits of non-native tree species, we suggest that some level of altered forest food preference and/or food limitation for the bird is occurring. Kererū have been observed eating the leaves of 41 species of native plants and over 20 non-native species (Clout & Hay 1989). Willows and tree lucerne are both deciduous, and the latter is a nitrogen-fixing species, so they are likely to have higher leaf nitrogen (and thus protein) concentrations than most native tree species, which are largely evergreen (Brandt et al. 2021). The few native tree species that have high nitrogen concentrations, such as hohere (*Hoheria populnea*), and the nitrogen-fixing kōwhai (*Sophora* spp.) were historically common in alluvial forest ecosystems, but these have been cleared for farming. This has reduced early spring sources of protein from native trees, and non-native trees have filled that role in the seasonal diet of kererū. However, practitioners firmly believe fruits from non-native tree species to be inferior for kererū dietary needs because the birds do not fatten to the same extent as they did when foraging on native forest species such as toromiro, tawa, and hīnau. The importance of food supply for kererū is supported by evidence that demonstrated that kererū detections did not always increase following predator control, which suggests that food supply at some sites may have been an important limiting factor (Carpenter et al. 2021). Therefore, the restoration of key native tree species that are palatable to kererū is a critical issue that will need be resolved if populations are going to be successfully restored to historic abundances in Tuawhenua and Whirinaki forests.

Effects on seed dispersal processes

The profound reductions in fruit availability and fruit size observed by practitioners in the last few decades have almost certainly impacted seed dispersal processes. Declines in both fruit abundance and kererū, which is a key seed disperser for Aotearoa's largest seeded plant species, must have led to fewer seeds being moved around the landscape. It is also possible that some degree of threshold relationship between kererū densities and the spread of seed from native fruit trees may have historically existed. Historically during the toromiro season, kererū formed large foraging flocks (hundreds of birds per flock) and moved extensively around the landscape to feed (Lyver et al. 2008). However, declines in kereru populations and flocking behaviour may have had implications for seed distribution and the ecological roles of the bird in the forest (Innes et al. 2022).

The declining size of fruits over time observed by practitioners could have mixed implications for seed dispersal. Large-seeded species like tawa and hīnau are often beyond the gape size of smaller avian frugivores (e.g. pihipihi [*Zosterops lateralis*]). For example, fruit size distributions of tawa from two South Island sites showed that between 25% and 60% of their fruit were within the gape range of kōkō, whereas no fruit were within the gape range of the smaller kōparapara (*Anthornis melanura*; Kelly et al. 2010). Therefore, smaller fruits are likely to expand the diversity of frugivores that are able to consume them and potentially create more diverse and resilient seed dispersal networks for these plant species. However, this potential benefit could be undermined if smaller seeds lead to decreased recruitment due to increased desiccation or lack of competitive advantage as seedlings.

Consequences of changes in fruit biomass for below-ground subsystems

All plant material that enters the below-ground subsystem does so either directly as litterfall or indirectly through herbivore activity. In the context of fruiting trees, those fruits that are not consumed by birds accumulate as litter on the soil surface, particularly during masting years, where they can impact ecosystem functioning in multiple ways (Fig. 3). Pulsed input of resources to the soil has been recognised as an important driver of nutrient fluxes in several ecosystems (Yang et al. 2008), and the deep layers of fallen fruits on the ground historically reported by the Tuawhenua and Ngāti Whare practitioners are likely to have served as substantial pulses of nutrients to the below-ground subsystem that have since declined over time. For example, reports of tawa berries that were two inches (5 cm) deep across the ground would involve about 1800 fruit per m^2 (assuming a mean fruit size of 28 mm × 19 mm). Assuming the dry mass of each fruit was 1.3 g (Yukich Clendon 2022) and that its nitrogen concentration was 1.7% (as reported for the congeneric *Beilschmeidia recurva*; Grubb et al. 1998)

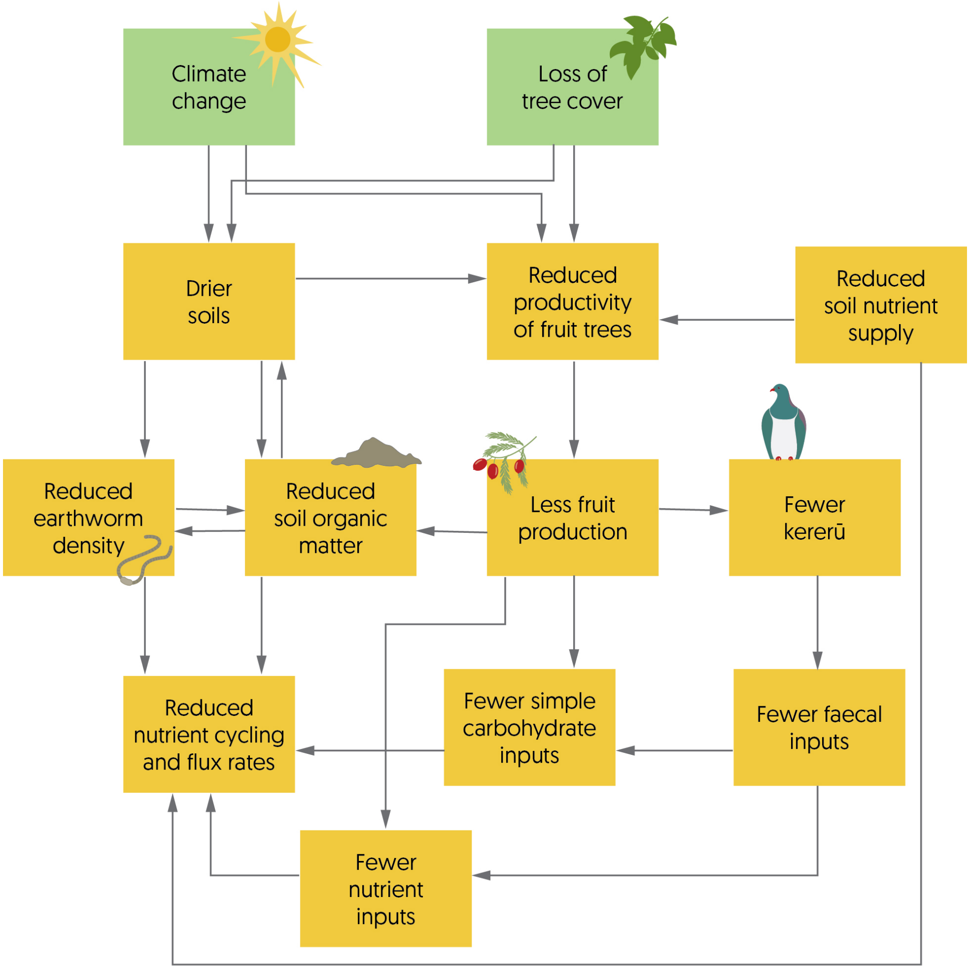

Figure 3. Multiple pathways through which reduction of fruit tree productivity and fruit production, as caused by loss of tree cover and climate change, impair below-ground processes that drive soil nutrient supply and plant performance.

then this would equate to a N content of 40 g N m^{-2}. This is significantly in excess of the N that is likely to fall as total litterfall in most of the world's forests (Shen et al. 2019) and 1–2 orders of magnitude higher than previous reports of N input from forest fruit fall elsewhere (e.g. Henkel & Mayor 2019).

Even if these deep layers of tawa fruit had only occurred in localised patches, the amounts of N input combined with the fact that nearly a third of the fruit mass is pulp (Yukich Clendon 2022), which is likely to be rapidly decomposed, suggests that the nutrients in the fruit represented a major component of the forest nitrogen cycle and a rapid source of nutrient supply for the trees. Further, the sugar content of the fruit pulp (Jana Prado 2012) is likely to have had a large priming effect on soil microbial activity (Bernard et al. 2022) which would have further promoted soil decomposition processes and thus tree nutrient supply. In addition, a dense layer of fruit on the ground would have likely led to much greater moisture retention in the upper soil, both through insulation and by conversion of fruit materials into soil organic matter. This aligns with historical reports from the practitioners of both moister conditions in the forest floor and higher densities of burrowing earthworms, with the latter likely having been promoted through greater availability of both soil moisture and food derived from berries. Burrowing earthworms are well recognised as major drivers of decomposition processes, soil nutrient supply, and plant growth (Blouin et al. 2013), so probably further contributed to tree productivity.

A further avenue for the return of fruits to the below-ground subsystem would have occurred indirectly via faecal material and dead bodies of frugivorous birds such as kererū. While we lack data for the basis of a quantitative estimate of this return, faecal return of nutrients from birds is widely recognised as an important driver of ecosystem nutrient fluxes, particularly underneath trees in which birds roost (Fujita & Koike 2007). Given the high amounts of labile nutrients in the faecal material from kererū and the historical high densities of kererū that were present prior to the 1970s (Lyver et al. 2008), we expect that the fertilisation of the forest floor through fruits entering the soil system indirectly via kererū would also have been a substantial driver of soil fertility, nutrient supply to the trees, and ultimately tree nutrition and growth (Fig. 3).

Consequences of changes in fruit biomass and phenology for feral pigs

Fruits of tawa, hīnau, and pirita together made up one-third of the diet of feral pigs in Te Urewera forests during the early- to mid-1980s (Thomson & Challies 1988). We suggest that these dietary fruit intake estimates are conservative because they were measured while fruit crops in Te Urewera were declining. The increasing propensity for feral pigs to excavate the forest floor with the decline in fruit biomass aligns with findings that pigs are more likely to disturb soil in search of below-ground foods (e.g. earthworms, roots) when above-ground foods are most scarce (Ballari & Barrios-García 2014). Foraging behaviour of feral pigs, particularly rooting, can remove vegetation, perturb soil structure, influence nutrient availability, and cause short-term reductions in seedling and/or sapling species richness (Hone & Robards 1980; Engeman et al. 2005; Krull et al. 2013). These impacts can also be exacerbated when pigs return to previously disturbed areas to re-disturb them (Krull et al. 2013), extending the extent of the impacts and the associated alteration of ecological processes. Similarly, recent evidence indicates that feral pig activity influences community composition and favours non-native plant species establishment within Hawaiian forest understories (Peyton et al. 2024). A general drying of the forest and loss of soil organic matter may have also impacted feral pig condition. Ground disturbance by feral pigs is influenced in part by their ability to disturb the ground, which is related to the penetration resistance of the soil (Hone 1988), and productivity of the soil ecosystem. Moist soils are generally less compacted (i.e. have lower penetration resistance) and have higher productivity (Wardle 2002) than drier soils; therefore we predict that the loss of fruit and the resulting decline in moisture and organic matter status of the soil (Fig. 3) may have impacted the physical ability of feral pigs to forage, and also reduced the abundance and availability of food sources on the forest floor and in the soil.

Consequences of changes in fruit biomass and phenology for cultural systems

Alterations in fruit abundance and phenology can directly impact the livelihoods and cultural systems of Indigenous communities (Shivanna 2022). Customary practices associated with the acquisition of food by some communities are highly cyclical and are conducted according to seasonal patterns in the weather, animal reproduction and migration, and plant growth (Turner & Reid 2022). Climate-driven shifts in phenological events can therefore have cumulative and cascading effects on cultural systems (Nakashima et al. 2012; Prevéy et al. 2020). The Lun Bawang and Penan peoples of Sarawak in Malaysian Borneo have used sightings of fruits and animals to predict the coming of different seasons and forecast the abundance of game (Hosen et al. 2020). However, increased climatic variability (e.g. drought and associated wildfires, heavy rainfall and associated flash flooding) has meant that the bio-climatic knowledge and indicators used by some Sarawak communities to forecast weather and seasonal cycles are less reliable now than they were historically, and are in danger of falling into disuse. To alleviate these effects, Sarawak communities have adapted a number of land management strategies such as the integration of animal husbandry with crop cultivation and shifting cultivation (Hosen et al. 2020).

Historically in Te Urewera, Tuawhenua dried and pounded tawa and hīnau fruit pulp and kernels into powder to make a porridge or bread (Best 1942; M. Ripia, Tuawhenua practitioner, pers. comm. 2013). Raw ripe fruits of makomako, kōtukutuku, tawa, and kahikatea were also commonly eaten. These fruits (and notably tawa) are now consumed much less frequently because of declines in fruit crops, highly variable timing of ripening, poorer size and quality of fruit, and the increasingly unappetising taste of fruit due to its stronger turpentine or astringent flavour. Fruit ripening in toromiro was once used as a key indicator by Tuawhenua and Ngāti Whare of when to harvest kererū. While the practice of harvesting kererū has declined dramatically relative to the past (Lyver et al. 2008), the cultural importance of the species to Tuawhenua means that processes linked to it, such as the ripening of toromiro and increased variability in the timing of ripening, are still relevant and observed by practitioners.

Indigenous languages are critical to expressing and connecting to beliefs, values, knowledge, nature, kinship, practice, and place (Wehi et al. 2024). They provide a place-specific relational way of naming, seeing, and understanding the environment (Chiblow & Meighan 2022). The harvest of forest fruits, and the culturally important food species reliant on fruit (e.g. kererū), were critically important to the maintenance and transmission of Tuawhenua and Ngāti Whare forest knowledge-language systems. Engagement with these food sources facilitated specific language use to describe the state and condition of fruit, with nuances to describe changes in the seasonality of fruit important for decision-making within customary management (e.g. deciding whether a kererū harvest should proceed, and if so, when and where to focus efforts). Importantly, the harvest of kererū provided a cultural context for the use of language which is now uncommon. Practitioners recognised that a declining use of traditional terminology for fruit coincided with a reduction in fruit and its use in the forest, declines in kererū populations, and a government prohibition that deterred harvesting. However, monitoring of kererū and forest processes (e.g. timing of fruiting) does offer a mechanism by which practitioners remain in regular contact with the forest (Lyver et al. 2018), in turn revitalising knowledge and language until such time as kererū populations are restored and legislation reformed. It also raises a question for practitioners about the role of introduced feral pigs and their harvest in revitalising knowledge-language systems relating to forest fruit. As baselines for biodiversity shift over time, historic language becomes increasingly important as a record of past ecological states, and for future goal setting and decision-making (Unasho 2013). Increasingly, Indigenous language-based institutions, such as Kura Reo taiao and whare wānanga around the country, emphasise the key role of language in the relationship between culture and the environment. These institutions are not only becoming vehicles for revitalising cultural-linguistic systems, but are also protecting and managing biodiversity.

Conclusion

The most recent evidence and projections indicate that the frequency and intensity of climatic extremes will increase during the 21st century. These changes are likely to significantly alter flowering and fruiting events in native forests, which are frequently cued by seasonal patterns of temperature and moisture availability (Butt et al. 2015). The ability to source traditional foods contributes strongly to food security, but also to cultural wellbeing by reinforcing the relationship of communities with their environment and its people (Turner & Turner 2008; Wehi et al. 2023). While the direct and indirect effects of changes in plant phenology are likely to impact daily intake and nutritional requirements of Indigenous and local communities, there can be much wider cascading effects on cultural practices and activities. Reduced interaction of communities with their traditional foods can create conditions for the loss of connection to place, elements of identity, language, and knowledge retention, and local rules and practices for protecting and using species (Lyver & Tylianakis 2017). In some instances, these impacts can happen rapidly and within one or two human generations. Even so, Indigenous communities around the world are adapting knowledge, practices, and livelihoods in response to changing climate and biophysical conditions. For Tuawhenua, in the absence of kererū, the harvest of introduced ungulate species creates a reason and incentive for practitioners to be in the forest, and provides an opportunity to gain insights into forest ecosystem state and dynamics. However, there is a trade-off in that these ungulate species can extensively damage native vegetation and landscapes in high densities and hinder the recovery of forest systems, indirectly reducing kererū populations. In a comparable study, rapid climate warming in the north-west Arctic region was found to have caused increased variability in the biophysical environment, requiring local people to adapt their practices (Krupnik & Jolly 2002). In the north-west region of the Yukon-Kuskokwim Delta, western Alaska, Yup'ik and Cup'ik harvesters overwhelmingly agreed that berries were ripening earlier in the season than in the past (Herman-Mercer et al. 2020); for example, cloudberries (*Rubus chamaemorus*) were ripening roughly a month earlier than previously. This period of earlier ripening overlapped with the period of subsistence and commercial salmon fishing in the region, requiring families to trade-off in engaging in one or other of the activities or attempting both at once (Herman-Mercer et al. 2020). As climate change intensifies it will continue to disrupt seasonal cycles of plants and wildlife, and traditional knowledge of species abundance, productivity, and phenology will therefore become increasingly important for forecasting future abundance, redistribution, and phenology of species. As such, adaptive, place-based management practices and responses to mitigate climate-mediated changes will be increasingly necessary (Ford et al. 2020).

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Additional information and declarations

Author contributions: PO'BL, PT, BT and DBC conceived the idea and designed the study; PO'BL, PT and BT conducted, translated and transcribed the interviews; PO'BL and PT did the analysis and verification; PO'BL, PT, JKC, DAW, and SJR wrote the manuscript, with editorial contributions from BT and DBC.

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Supplementary material

Additional supporting information may be found in the online version of this article.

Appendix S1. Tūhoe Tuawhenua plant names and corresponding species of kererū food sources in Tuawhenua region of Te Urewera.