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Indigenous plant naming and experimentation reveal a plant–insect relationship in New Zealand forests

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Abstract

Drawing from both Indigenous and "Western" scientific knowledge offers the opportunity to better incorporate ecological systems knowledge into conservation science. Here, we demonstrate a "two-eyed" approach that weaves Indigenous ecological knowledge (IK) with experimental data to provide detailed and comprehensive information about regional plant–insect interactions in New Zealand forests. We first examined Māori names for a common forest tree, *Carpodetus serratus,* that suggest a close species interaction between an herbivorous, hole-dwelling insect, and host trees. We detected consistent regional variation in both Māori names for *C. serratus* and the plant–insect relationship that reflect *Hemideina* spp. abundances, mediated by the presence of a wood-boring moth species. We found that in regions with moths *C. serratus* trees are home to more wētā than adjacent forest species and that these wētā readily ate *C. serratus* leaves, fruits and seeds. These findings confirm that a joint IK—experimental approach can stimulate new hypotheses and reveal spatially important ecological patterns. We recommend that conservation managers partner with local IK-holders to develop two-eyed seeing approaches that weave IK with quantitative data to assist planning and management. Next steps in our system could include assembling IK species names within each locality to construct a multilayered understanding of local ecosystems through an IK lens.

KEYWORDS

Carpodetus, herbivory, Indigenous knowledge, mātauranga Māori, orthopteran, pūriri moth, seed dispersal, seed predation, traditional ecological knowledge, tree weta

1 | INTRODUCTION

During a time of ecosystem change and biodiversity loss, there is increasing demand to develop ecological management strategies from multiple sources of knowledge (Sutherland et al., 2013; Tengö et al., 2017). One such source is Indigenous knowledge (IK), drawn from intergenerational observations and experience of Indigenous peoples over centuries (Berkes, 2008; Huntington, 2000). Eighty percent of the world's biodiversity occurs on lands managed by Indigenous peoples (Garnett et al., 2018); as such, conservation partnerships that weave IK with quantitative data provide a valuable approach that could not only improve understanding of species interactions and ecological systems, but also add value to conservation planning and practice. Many conservation decision-making processes, for example, require distributional data that may be embedded in IK (e.g., Service et al., 2014).

"Two-eyed seeing" is a term first described by First Nations Mi'kmaq elder Albert Marshall as "To see from one eye with the strengths of Indigenous ways of knowing, and to see from the other eye with the strengths of Western ways of knowing, and to use both of these eyes together" (Bartlett, Marshall, & Marshall, 2012). Such approaches bring together Indigenous and Western ways of knowing to meet environmental challenges, improving, for example, our identification and understanding of species interactions, past and current distributions, and ramifications of range shifts (Service et al., 2014). Utilizing both systems can yield more comprehensive and detailed information than that gained from either system alone. Experimental studies that complement IK therefore also potentially assist the inclusion of IK in conservation management, by providing additional quantitative data and fine-scale detail that may not otherwise be evident (Kutz & Tomaselli, 2019).

Feeding relationships are critical to species interactions and ecosystem functioning, but information on these may be lacking, particularly where invertebrates are concerned. For example, herbivorous insects living in rain forests are part of the most diverse food web in the world (Morris, Lewis, & Godfray, 2004; Paniagua, Medianero, & Lewis, 2009), and it is difficult to describe all the trophic interactions that structure these communities. Less is known about insects than almost any other multicellular phylogenetic group, despite their abundance. However, observations of feeding relationships often appear in IK, and can provide a basis for investigating potential food webs (e.g., Egeru et al., 2015; Wehi, Cox, Roa, & Whaanga, 2013). Here, we present an example of a two-eyed seeing approach from New Zealand, that identifies species interactions embedded in Indigenous plant names, explores regional distribution data, and applies Western scientific tools to gain detailed data on feeding relationships, thus generating additional quantitative data to assist conservation management.

Many insects use holes in the trunks and branches of trees as daytime refugia (Trewick & Morgan-Richards, 2000) and in New Zealand, nocturnal tree wētā (*Hemideina* spp.; orthoptera) are one of the most common groups to do so in lowland forests. Tree wētā (adult weights 2–6 g) likely play a pivotal role in forest ecosystem functioning by contributing to ecosystem services such as seed dispersal, nutrient cycling and herbivory (Duthie, Gibbs, & Burns, 2006; Griffin, Trewick, Wehi, & Morgan-Richards, 2011), but details are lacking. In the Indigenous Māori language, the common forest tree *Carpodetus serratus* has a number of names, four of which refer to the endemic tree wētā (hereafter "wētā"), suggesting a close association between plant and insect. *Hemideina* species are morphologically similar (Figure 1) and all rely on wood boring invertebrate species such as long-horned kānuka beetle larvae (*Ochrocydus huttoni*) and the caterpillars of pūriri moths (pepetuna, *Aenetus virescens*) to construct the holes they use as refugia (Ordish, 1992; Sandlant, 1981). The arboreal wētā emerge from these holes at night to browse on foliage (Kelly, 2006; Moller, 1985; Ordish, 1992; Wehi, Jorgensen, & Morgan, 2015). Despite often small entrance holes (widths often 9–13 mm diameter; Field & Sandlant 2001), occupancy of refugia may range from none to many wētā (Field & Sandlant 2001; Moller, 1985; Kelly, 2006). In turn, prior studies of fruit consumption and defecation of intact seeds argue for adaptive associations between wētā and some native plant species (Duthie et al., 2006; Morgan-Richards, Trewick, & Dunavan, 2008). However, this association might be costly to plants because a large proportion of seeds may be destroyed by insects after ingestion (Schupp, 1993; Wyman, Trewick, Morgan-Richards, & Noble, 2011).

We began by investigating all known Indigenous Māori names for *C. serratus*, and assessed whether these names have regional or universal distribution in New Zealand. Because only some of the Māori names for *C. serratus* suggest a close association between wētā and the plant, we sought evidence for regional variation in the species' interaction. We used the Indigenous name "putaputawētā" (meaning many insects emerging) to predict that *C. serratus* is home to more wētā compared to adjacent forest tree species, either by providing more refuge holes, and/or by having a higher proportion of holes used by wētā. To investigate costs and benefits of wētā infestation, as suggested by an alternate Indigenous name "kaiwētā" (meaning wētā food), we estimated the quantity of *C. serratus* leaves eaten, the proportion of *C. serratus* material in wētā frass from individuals collected on *C. serratus*, and tested the fate of seeds when fruits are eaten by wētā. Finally, we considered the experimental results in light of IK about species interactions and regional distributions.

2 | METHODS

2.1 | Study system and sites

We studied the relationship between *C. serratus* and wētā at three forested locations in North and South Island New Zealand (Figure 1). In the Urewera Forest (Owaka;

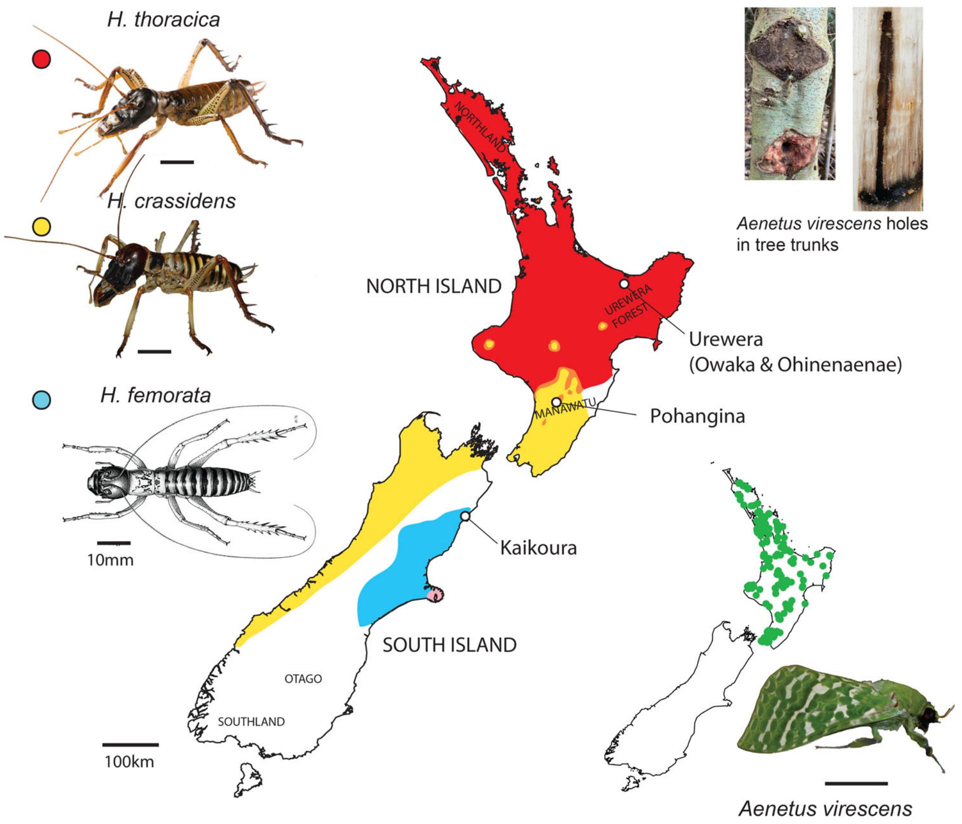

FIGURE 1 Distribution of three New Zealand tree wētā species (*Hemideina thoracica* red, *H. crassidens* yellow, and *H. femorata* blue) with field sites and locations mentioned in text. The distinctive external holes created by the caterpillar of the pūriri moth (*Aenetus virescens*) are shown at top right, together with the internal cavity bored in the tree. The moth distribution based on i-Naturalist records is shown at bottom right. Scale bars for insects = 10 mm

38°12′8.9″ S, 176° 59′40″ E and Ohinenaenae; 38° 12′ 8.7″ S, 177° 0′ 7.4″ E), the local wētā species is *Hemideina thoracica*, and at Pohangina in the Manawatū (40°18′S, 175°79′E; 40012′S, 175 85′E) the wētā is *Hemideina crassidens*. In South Island, at Kaikoura (Fyffe Palmer Scenic Reserve; 42° 19′ 49.656″ S 173° 38′ 16.8648″ E), the local wētā species is *Hemideina femorata*. These species are sufficiently similar in both refuge behavior and ecology that Māori apply the name (wētā) to all tree-inhabiting *Hemideina*; the morphological and ecological likenesses are similarly noted in the taxonomic history of this genus (Ramsey & Bigelow, 1978). These insects are large (adult body length ~ 35–40 mm; Field & Sandlant, 2001), hemimetabolous, nocturnal and common across most of New Zealand (Figure 1).

C. serratus J.R. Forst et G. Forst. 1776 (Rousseaceae) is an evergreen, endemic tree common in lowland and montane forest over the whole of New Zealand. The species grows up to 10 m with a knobbly barked trunk up to 30 cm diameter. Fruits are retained green on the tree from the previous season, and ripen from autumn to spring to small, purplish black, soft berries (Burrows, 1996). Each fruit contains many seeds small enough for tree wētā to swallow whole (fruits 1–1.7 mm; Duthie et al., 2006). Birds eat the fruit, and disperse the seeds (Burrows, 1996). In North Island, the caterpillar of the moth *A. virescens* is a major contributor to hole formation in trunks and branches of *C. serratus*. However, this moth species is absent from the entire South Island (Figure 1).

2.2 | Ethics

The application of “two-eyed seeing” as a guiding principle bridges the divide of understanding between Indigenous and Western researchers, knowledge and processes. We affirm our support for retention of biocultural knowledge-by-knowledge holders and recognize Indigenous rights and connections to traditional territories. In the Urewera forest, we presented the project proposal to the Ruatoki tribal science committee. Fieldwork was conducted on Māori land in the Urewera in partnership with tribal members, on public land in the Manawatū with permission of Palmerston North City Council, and in South Island under a Manaaki Whenua Landcare Research global research permit.

2.3 | IK records

Human settlement of New Zealand began with the Indigenous Māori people around 800 years ago, and New Zealand-specific IK has grown since that time. We first spoke to knowledge holders in our extended family and from local tribes (iwi), and recorded the names they used for *C. serratus* (Table 1). However, because European colonization ca. 200 years ago has had deleterious effects on knowledge systems, historical manuscripts and other written documents have become important sources from which to reclaim IK. We thus searched archival records for information on *Carpodetus* using the following terms: marbleleaf, putaputaweta, *Carpodetus*, kaiweta. Archives included Papers Past (the National Library of New Zealand's online repository of early New Zealand newspapers), magazines and journals https://paperspast.natlib.govt.nz/, letters, diaries, and parliamentary papers.

2.4 | Tree species, tree hole sizes, and use by wētā

We compared the number of holes in *C. serratus* trunks and the relative rate of occupancy of these holes by marking a set of *C. serratus* trees at each location, and selecting adjacent trees of other species matching size and proximity to each *C. serratus* (Urewera $n = 26$ for *C. serratus* and $n = 60$ for adjacent trees; similarly, Pohangina $n = 3$ and $n = 5$, and Kaikoura $n = 50$ and $n = 64$, respectively). We excluded seedlings and very small trunked trees with no holes. Spatial distribution of tree holes varies with tree size and species in New Zealand forest (Blakely et al., 2008; Blakely & Didham, 2008); hence, we standardized our methods to include holes within a similar tree height range, and included diameter at breast height in our models. For each tree, we measured diameter at breast height, and counted all holes present from ground level up to a height of ~3 m (see Supporting Information). For the first 50 tree holes found in *C. serratus*, and 50 holes on other tree species, we measured the height and width of hole entrances and height above ground. To determine whether wētā were in tree holes we recorded nocturnal activity at these 100 holes at each of the three sites. Cotton thread was fixed tautly across hole entrance with duct tape, so if a wētā were to exit, the thread would be pushed aside and tension lost. We checked each threaded hole for five consecutive days. In a preliminary trial to ensure that this method was reliable, we found that thread measurements provided reliable estimates of relative rate of hole use by wētā (Supporting Information).

2.5 | Wētā herbivory

To better understand the association between *C. serratus* and wētā, we conducted captive feeding trials to estimate the quantity of leaf material eaten nightly by wētā. We collected *H. crassidens* at random with respect to sex and size ($n = 41$; mean weight 2.33 g, range 0.2–5.4 g). Each wētā was kept in a separate container at constant temperature (14°C) and provided daily with fresh *C. serratus* leaves. Leaf consumption over seven consecutive nights was estimated by digitally scanning each leaf before and

TABLE 1 Māori names for the tree *Carpodetus serratus* and notes on their regional use where known

Name used	Etymology	Region	Source
Putaputawētā	*Putaputa*, to emerge. The double usage adds emphasis, suggesting many emergences *Wētā*, the insect	Widespread Used by many North Island iwi (tribal groups)	Personal communication T.W Harawira, P. Te Ngaru
Putawētā	*Puta*, to emerge *Wētā*, the insect		
Kaiwētā	*Kai,* food, feeding *Wētā*, the insect	Urewera Used by Tūhoe iwi	Best (1908), Fenwick (1925), Lyver, Taputu, Kutia, and Tahi (2008) Personal communication T. W. Harawira
Punawētā	*Puna*, a source of *Wētā*, the insect	Stewart Is?	http://maoriplantuse.landcareresearch.co.nz/
Piripiriwhata Piripiriwata Piripiriweta	*Piripiri*, hanging ferns such as spleenworts (*Asplenium* spp.) that often grow on tree trunks *Whata*, to be suspended	Otago, South Is Northland Central North Is, South Is	Buchanan (1869) Cunningham 1820s (Herbaria specimens Te Papa WELT SPO79466, 79477), Anonymous (1896), Anonymous (1906), Anonymous (1917)

Note: Names and meanings sourced from the online Māori Dictionary, https://maoridictionary.co.nz/ (keyword = marbleleaf) and http://maoriplantuse.landcareresearch.co.nz/.

after eating, with area reduction used to infer how much each wētā ate per night. Surface area was determined with the software Compu Eye Leaf and Symptom Area (Bakr, 2005). To convert leaf area eaten into leaf volume (dry and ash weight) we scanned 20 fresh *C. serratus* leaves before they were dried, weighed, and burnt at 500°C for 6 hr. We also opportunistically analyzed the frass of 10 wētā living on *C. serratus* trees, to determine what proportion of their diet consisted of *C. serratus* leaves or fruit. Between 2 and 13 slides were made from a 40 ml subsample of the frass of each individual. For each slide, five fields of view were scored to estimate the proportion of *C. serratus* cells and other material present.

2.6 | Wētā frugivory and seed predation

To investigate whether wētā are seed predators or potential dispersers, we collected five ripe bunches of *C. serratus* fruit from three locations (North Island 40°18′S, 175°79′E; 39° 40′ S 177° 1′ E; South Island 45°21′56.2″S, 170°43′02.2″E). We weighed five randomly selected ripe fruit per bunch. For each fruit, we measured length and width on the longest axis, separated all seeds, and recorded number and size (length and width; see Supporting Information).

We estimated the proportion of seeds passed intact through wētā in captive feeding trials. Wētā were kept in captivity in conditions described by Wehi, Raubenheimer, and Morgan-Richards (2013). Sex, femur length, and weight were recorded for each wētā and each individual was used in only one trial. We pre-fed carrot to experimental wētā for 2 days to ensure there was no retention of previous foods (including seeds) in the gut, then provided either a whole or half *C. serratus* fruit. In the first trial, we fed wētā whole fruits of known weight. In the second trial, we halved each fruit, weighed both halves, then one half was fed to the wētā. From the other half of each fruit we counted all seeds to estimate total number of seeds, then used these seeds as controls in germination trials. Sixty-four wētā (36 females and 28 males) ate some or all of the fruit offered. After 12 hr, we collected uneaten fruit from each wētā container and recorded the number of seeds in any remaining pulp. We collected frass for the 6 days following the trial, and recorded number of intact and seed fragments. We calculated the likely number of seeds destroyed during the feeding trial (based on estimated seed number for half fruits), and thus the total proportion of seeds passed intact or destroyed from each fruit as a measure of wētā seed predation.

To determine the effects of wētā gut passage on germination, we placed all intact *C. serratus* seeds from wētā frass on moist filter paper in petri dishes in a 16°C temperature-controlled room in light conditions similar to Burrows' standard method (1996). We used intact seeds from half-fruits as a control and treated these identically. Watering was carried out as necessary. We checked seeds weekly for 5 months, and recorded date of germination based on radicle emergence.

2.7 | Statistical analysis

All statistical analyses were undertaken in R (R Core Team, 2012). Data and code are available in the Landcare Research DataStore data repository: DOI https://doi.org/10.7931/51hs-j779. To examine whether *C. serratus* has more refuge holes than neighboring forest trees, we compared data from two locations, Urewera and Kaikoura, but excluded Pohangina in the first instance because dbh was not recorded at this location. We used a zero-inflated Poisson model (zeroinfl function in the pscl package; Jackman et al., 2017) as data were overdispersed. The model included tree species (*C. serratus* or not), tree size (dbh) and location, with location also the regressor in the zero inflated part of the model. We then ran a general linear model without the dbh term but including data from the third location (Pohangina). We calculated confidence intervals using bootstrapping (2,000 replicates, boot function, boot package; Canty & Ripley, 2019). To compare rate of hole use by wētā between *C. serratus* and other tree species, we used a mixed effects model (glmer function, lme4 package; Bates, Maechler, Bolker, & Walker, 2014) with tree species (*C. serratus* or not) and location as fixed variables and individual trees as a random variable, and calculated Wald's confidence intervals. To examine whether there was a difference in refuge hole size between the holes of *C. serratus* and other trees, we used a mixed effects model with tree species (*C. serratus* or not) and location as fixed variables, and individual trees as the random variable (lme4, Bates et al., 2014). We calculated confidence intervals using bootstrapping. Finally, we examined the relationship between hole size and wētā presence with a further mixed effects model, with hole size and location as fixed variables and individual trees as the random variable, and calculated Wald's confidence intervals. To investigate the effect of wētā gut passage on seeds, we used a binomial model to test if the proportion of intact seeds was predicted by sex and weight. In this model, each individual weta represented a single germination replication. We used a linear model to test how long whole seeds were retained in the gut and a paired *t* test on log-transformed data to investigate whether passage through wētā guts significantly influenced germination of *C. serratus* seeds.

3 | RESULTS

3.1 | IK records

In our archival searches, we found five Māori names reliably recorded for *C. serratus* (Table 1). Of these, the first four include reference to wētā, with "puta" meaning to emerge, and "puna" meaning a source. In North Island, *C. serratus* is commonly known as putaputawētā. "Puta" refers to emergence (with the repeating syllables indicating many emergences), and "wētā" refers to all species within the genus *Hemideina*. Although the name putaputawētā is widespread, Māori language speakers still use alternative local names (Table 1) and tribal (iwi) variations in names occur in the archival literature.

The earliest written records we found (Buchanan, 1869) referred to *C. serratus* as "Piripiriwhata" in the context of a South Island location. But despite the possibility of southern origins for "piripiriwhata" that also align with its ecology (see below), we also found two herbaria specimens labeled with two names: "piri-piri-w[h]ata" and "piri-piri-weta" (Te Papa herbarium, specimens WELT SPO79466 and 79477). These specimens were collected from the very north of North Island in 1826 by English botanist Allan Cunningham (who spent less than a year in New Zealand). In contrast, the name "kaiwētā" is clearly located in the Urewera forest district, North Island (Best, 1908; Fenwick, 1925; Lyver et al., 2008) where it is still used today. Newspaper sources indicate that by the early twentieth century, some European settlers were using the name putaputawētā in South Island (e.g., Anonymous, 1898; Poppelwell, 1910), but others referred to putaputawētā as a "North Island name", and preferred the English name marbleleaf in South Island (McCaskill, 1937). Other articles show continuing use of the name piripiriwhata in Otago, South Island and elsewhere at this time, although punawētā or putaputawētā were frequently used in North Island descriptions (e.g., Anonymous, 1913; Anonymous, 1937; Turbott, 1937; Table 1).

3.2 | Tree species, tree hole sizes and wētā habitation

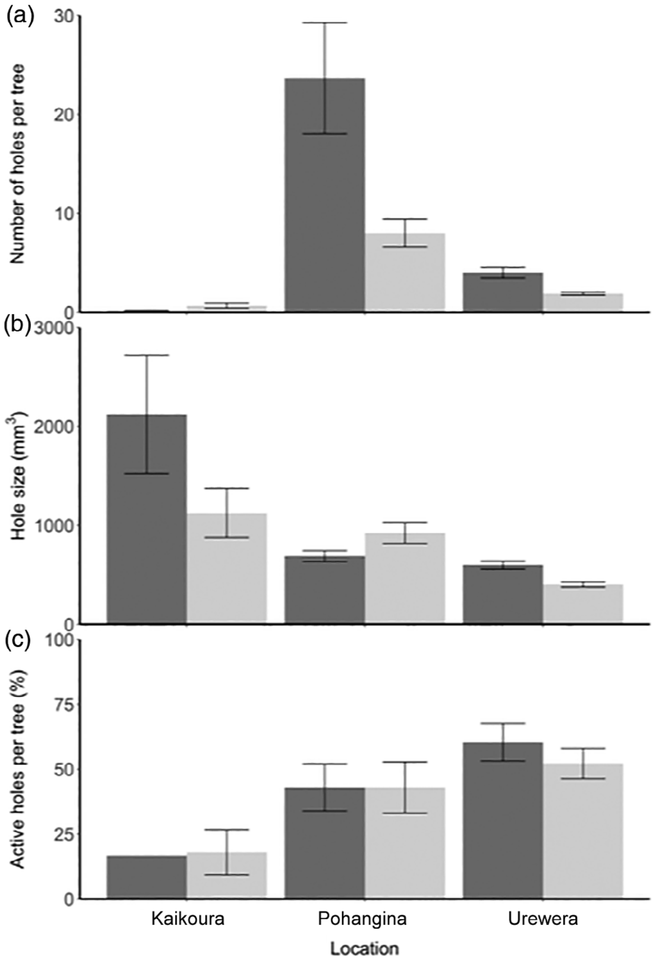

FIGURE 2 The number of refuge holes for insects (wētā), and their occupancy, varies by both location and tree species in New Zealand forest. (a) Mean number of holes by tree type and site (±*SE*). (b) Mean hole size by tree type and location (±*SE*). (c) Mean percentage of "active" holes per tree (i.e., occupied holes/total holes) ± *SE* (only one active hole in a putaputawētā at Kaikoura). Active holes are those where tree wētā occupancy is inferred from thread movement over holes over a 5-day period. Kaikoura is a South Island site, and both Pohangina and Urewera are North Island sites. *C. serratus* trees are denoted in dark gray, and other tree species in light gray

In North Island forests (where *A. virescens* are present; Figure 1), *C. serratus* trees had more holes in their trunks (below 3 m) than other species of trees (hole number in relation to tree species, size [dbh] and site: coef = 3.53, 95% CI: 2.58, 6.74, Figure 2a). In this model, trunk size (dbh) was unimportant. We found more holes in *C. serratus* trees than in adjacent trees of other species, and more holes at North Island locations (Urewera and Pohangina) than at Kaikoura in the South Island which lacks *A. virescens* hole-builders (Pohangina: coef = 5.1302, 95% CI: 4.42, 6.00; Urewera: 3.3, 95% CI: 2.66, 4.21; tree type [other]: −1.966, 95% CI: −2.81, −1.31). Hole entrances were significantly smaller and more consistent in size (Figure 2b) in the North Island compared to Kaikoura (Pohangina coef: −1,435.19, 95% CI: −2,110.85,

−638.72; Urewera coef: −1,457.97, 95% CI: −1996.37, −813.15). However, hole size was not a good predictor of wētā habitation (coef: −0.29, 95% CI: −1.00, 0.419). The number of "active" holes was highest when we monitored Urewera trees (significantly so, coef: 2.61, 95% CI: 0.17, 5.06), and lowest at Kaikoura, but we did not find a significant difference in relative rate of hole use by wētā between *C. serratus* and other tree species at each site (Figure 2c).

3.3 | Wētā herbivory

The amount of *C. serratus* leaf tissue eaten by captive tree wētā was related to wētā size (Figure S1). On average, wētā ate about 700 mm^2 of leaf per gram of body weight per night. From our fieldwork, we estimated there would be at least eight wētā foraging on each *C. serratus* tree in North Island forests, resulting in an average loss of about 22 leaves per tree per night to herbivory if wētā feed on the tree where they reside. We observed *C. serratus* cuticle cells in the frass of nine of 10 wētā living on *C. serratus*. The proportion of material in their frass was approximately 72% ± 8.6 (mean ± *SE*) *C. serratus* and 28% other plant species and insect parts.

3.4 | Wētā frugivory and seed predation

C. serratus fruit and seed did not vary significantly in size among locations and all seeds were small enough to be swallowed whole by adult *Hemideina* (see Supplementary Information and Table S2). Although captive *Hemideina* readily eat fruit, few seeds were passed intact (generally less than 10%, or up to five seeds; Figure 3). There was no relationship between wētā weight and proportion of whole seeds passed (weight: coef 0.11, 95% CI: −0.037, 0.257; Figure 3), but males passed a greater proportion of whole seeds than females (male: coef 1.52, 95% CI: 1.13, 1.93). Most seeds were expelled within 4 days of feeding, and there was no relationship between number of whole seeds passed and time spent in the gut (i.e., days since eating: $F_{1,53} = 0.066$, $p = .7978$, see Figure S3). Although more of our control seeds germinated (25.05%) than the seeds that had passed through wētā (13.26%), these germination rates did not differ significantly (13.36% ± 4.83, $n = 100$ seeds after weta passage; 25.05% ± 8.41, $n = 98$ not eaten controls; paired *t* test: $t = 0.47647$, $df = 21$, $p = .6387$, Figure 4).

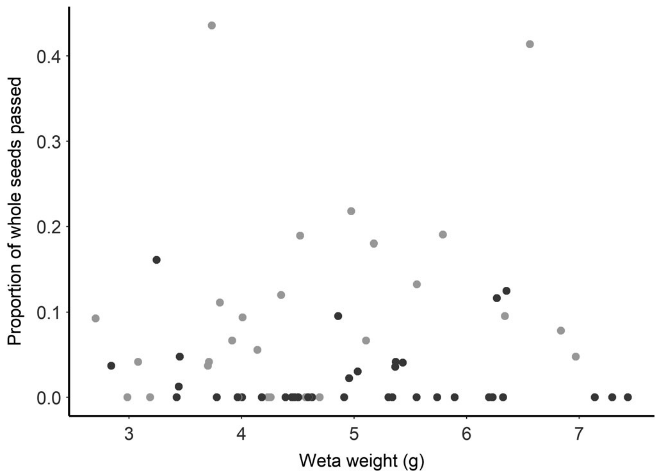

FIGURE 3 Proportion of whole *Carpodetus serratus* seeds passed through a tree wētā (*Hemideina crassidens*) gut intact, in relation to wētā weight (grams). Female wētā are denoted as dark dots, and males as light gray dots

4 | DISCUSSION

4.1 | Indigenous names and ecological observations for *C. serratus* and wētā

The ecological information embedded in the Māori names for *C. serratus*, that translate to many wētā emerging or the source of wētā (putaputawētā, putawētā, and punawētā), led us to collect and analyze data on the association between *C. serratus* and wētā (*Hemideina* spp.), including potential costs and benefits for the tree. In North Island forests, between 40 and 60% of tree-trunk holes contain wētā during the day, and *C. serratus*

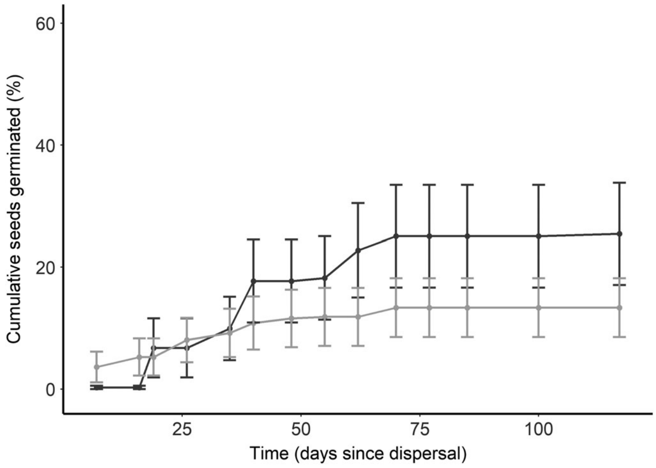

FIGURE 4 Being eaten by a wētā does not improve rate of germination of putaputwētā seeds in laboratory conditions. Cumulative mean (±1 *SE*) percentage of intact *Carpodetus serratus* seeds germinated over 117 days. Black dots represent control seeds not passed through tree wētā (*Hemideina crassidens*), and gray dots represent seeds eaten and found intact in tree wētā frass

provide more potential refuge holes for wētā than adjacent forest tree species. All holes on northern *C. serratus* in this study were bored by *A. virescens* (pūriri moth) caterpillars and subsequently occupied by wētā. The South Island absence of *A. virescens* resulted in fewer refugia for wētā on all forest trees, *C. serratus* included, compared to North Island locations. This result is compatible with the predominantly southern Indigenous tree name (piripiriwhata) that does not refer to an association with wētā.

In the Urewera forest, where recorded tree wētā occupancy was highest, the Indigenous name for *C. serratus* is kaiwētā, suggesting the plant provides food for the insect. Herbivores affect both carbon and nutrient cycles in temperate and tropical forests (Metcalfe et al., 2014), and it appears that wētā herbivory could play a substantial role in New Zealand lowland forests. The sheer number of refuge holes on *C. serratus* trees in North Island in particular means that individual trees may support a large number of wētā at any one time, resulting in loss of foliage and potentially fruit. Griffin et al. (2011) estimated that individual wētā consumed between 20 and 500 g of leaf material a night per hectare; our frass analysis suggests that wētā living on *C. serratus* trees are likely to eat locally, resulting in considerable loss of foliage, as well as potentially fruit, from a host tree.

In captive experiments, wētā readily ate the fruits and passed only c. 10% of *C. serratus* seeds intact through their gut. Most seeds passed through wētā within 4 days (Figure 4) and almost all were severely damaged. These high rates of destruction suggest that wētā have a negative effect on seed success (see also Duthie et al., 2006). In forests, ripe fruit is often present on *C. serratus* for long periods (Burrows, 1996), so benefits to seed predators could accrue over long time periods, although fruit size is small when compared to other New Zealand plant species (see Figure 3 and Kelly et al., 2010). Of the intact seeds, few germinated, and there was no difference in germination rate between eaten and non-eaten seeds (cf. Duthie et al., 2006). In contrast, gut passage in some birds has significant positive effects on germination (e.g., Krefting & Roe, 1949; Wotton & McAlpine, 2015). Based on estimates of tree wētā movement (1–12 m per night; Kelly, 2006; Gwynne & Kelly, 2018) and site fidelity (see Supporting Information), we estimate that intact dispersed seeds are very unlikely to be deposited more than 40 m from a tree. This contrasts with seed dispersal by birds (e.g., Krefting & Roe, 1949; Trewick & Morgan-Richards, 2019; Wotton & McAlpine, 2015) where seeds are likely to result in dispersal distances of >100 m (Wotton & McAlpine, 2015). That is, disperser effectiveness of wētā, as measured both by treatment quality in the mouth and gut, and the probability of favorable seed deposition (see Schupp, 1993), is low. It is almost certain that we have underestimated the total number of wētā on each tree, given that there will also be many tree holes above 3 m that were not censused (Blakely et al., 2008). As well, our method of using thread displacement to estimate hole occupancy by wētā might underestimate numbers as we assumed single hole occupancy, even though some holes demonstrate multiple occupancy (Kelly, 2006; Sandlant, 1981; Wehi et al., 2015). Nonetheless, when used as a relative occupancy measure during the same time period (at the same location) to compare the use of holes in different tree species, this technique provides reliable evidence of relative rates at which wētā use tree holes as daytime refuges. Overall, our data suggest *C. serratus* trees have a higher than average load of wētā using them as a resource. Although there could be benefits in the interaction that were not tested here such as wētā eating other insect species, we did not detect a direct benefit to the tree from this association. Kai wētā is thus an apt description of the role of this tree species in the forest.

4.2 | Indigenous names and regional ethnoecologies

Our examination of Māori names for a common New Zealand forest tree *C. serratus* revealed regional variation in the use of these names. Four of these names embed observations of the insect wētā living in or feeding on this tree species. These names were/are predominantly used by iwi living in the North Island, matching our ecological observations of high numbers of wētā living in *C. serratus* in this region. Another Māori name for this tree, piripiriwhata, likely reflects ecological associations with epiphytes and we speculate that piripiriwhata was the preferred original name in southern areas where tree-trunk holes and wētā are less numerous but lianes and epiphytes are abundant (Wardle, 1991). This type of regional IK can potentially provide hypotheses of regional variation in species interactions useful for conservation managers in ecosystem assessments and monitoring.

Regional Indigenous name variants are common for flora and fauna in First Nation ethnobotanies (e.g., Turner, 2014). These names provide a rich vein of ecological knowledge that can be linked to species distributions, local interactions, and other ecological indicators (e.g., Lyver et al., 2008). Wohling (2009) notes that the scale and localization of IK is an important consideration that can add both value and confusion to environmental management. In this study, confusion in our understanding of Indigenous name variants, including the lack of geographically specific records available, results in part from language and IK loss since 19th Century European colonization in New Zealand. This post-colonization scenario is common in many First World nations. As well, there may be rich veins of IK held by local IK holders that we did not encounter in this study; the benefit of long-term partnership with such knowledge holders is clear (see, e.g., the extraordinary work on New Guinea flora and fauna (Majnep & Bulmer, 1977; Majnep & Bulmer, 2007). Nonetheless, our study clearly reflects that Indigenous names can suggest spatial and temporal species distributions and ecological relationships.

The use of a “two eyed seeing” framework thus provides a strong ecological basis from which to quantify new hypotheses of ecological functioning, and add to the detailed information required in both conversation practice and restoration ecology. Strong engagement with local scholars and communities will enhance this practice, add critical local insights, and lead to best practice conservation efforts (Rayne et al., 2020). Huntington's collaborative work with Inuit communities on whale population movements off Alaska is an enduring example of the critical conservation gains that can be made (Huntington, 1992). These issues are of particular importance, given that many critically threatened species, ecosystems and landscapes are also Indigenous homelands (see, e.g., Garnett et al., 2018).

Food web ecology is a critical issue for ecosystem functioning (Tylianakis, Didham, Bascompte, & Wardle, 2008) and thus for successful ecosystem conservation and restoration at landscape scales. Regional or temporal variance in species names, as reported here, is frequently built and maintained over centuries in IK, in contrast to scientific documentation or investigation that is often limited in space and time (Horstman & Wightman, 2001). As such, IK can offer both spatial and temporal ecological information critical to conservation processes. In New Zealand, for example, the honeyeater *Prosthmadera novae-seelandiae* is known by many Indigenous names, which describe changes in seasonal feeding patterns (Wehi et al., 2019). IK insights may also be useful for rare species or to help identify ecological interactions in past ecosystems with extinct species (e.g., Ziembicki, Woinarski, & Mackey, 2013), and systematic documentation of IK can result in early detection of ecological change, including population decline or loss of ecosystem function (Kutz & Tomaselli, 2019; Tomaselli, Kutz, Gerlach, & Checkley, 2018). Such gains are not necessarily limited to species names; ecological distributions identified from landscape wide modeling of Indigenous place names might also assist restoration of ecosystems and landscapes (Horstman & Wightman, 2001).

From the relevant ecological data that we have unpacked here in relation to *C. serratus* and wētā, we show that IK provides a rich vein of ecological knowledge that can lead to new insights. The types of data shown here reveal how IK can be complemented by numerical formats that quantify uncertainty and variability around observations (Kutz & Tomaselli, 2019), and mean that conservation management can be undertaken with increased confidence when knowledges align (Gagnon & Berteaux, 2009). Next steps in New Zealand systems could include examining regional nuances further, such as *C. serratus* trunk microhabitats which may provide rich fern and other species habitat as suggested by the southern IK name, to gain a better understanding of ecosystem differences. As well, assembling IK species names within each locality to construct a multilayered understanding of each forest ecosystem through an IK lens could create strong community partnerships with conservation managers, as well as better understanding of past and current ecosystems. A two-eyed seeing approach that values both experimental work and sources of IK also prepares a pathway for co-management by valuing community knowledge and participation, and is thus more likely to succeed (Service et al., 2014; Zimmerman, Peres, Malcolm, & Turner, 2001). Given the high percentage of biodiversity with Indigenous stewards and lands, a partnership approach that values IK together with western scientific approaches is a powerful step forward (Daly, Trewick, Dowle, Crampton, & Morgan-Richards, 2020; Moller, Berkes, Lyver, & Kislalioglu, 2004). Partnerships with Indigenous elders or other knowledge holders, whose understandings are grounded in specific localities, ecologies and geographies, are likely to offer unique insights about the demographies and ecologies of species and ecosystem function to improve conservation processes.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Priscilla M. Wehi initiated the study; Mary Morgan-Richards and Priscilla M. Wehi developed methodology; Priscilla M. Wehi and Mary Morgan-Richards conducted fieldwork and experiments; Gretchen Brownstein led data curation and statistical analyses, with input from Priscilla M. Wehi; Priscilla M. Wehi led the writing and editing, with critical input from both Mary Morgan-Richards and Gretchen Brownstein.

DATA AVAILABILITY STATEMENT

Data will be made available to all interested researchers upon request.

ETHICS STATEMENT

No ethics review for animal handling or human participant research was necessary for the work reported in this study.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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