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RESEARCH

When an enemy of an enemy is not a friend: Tri-trophic interactions between kākā, puriri moths and makomako trees

Kirsty J. Yule and Kevin C. Burns* (iD)

School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6012, New Zealand.
*Author for correspondence (Email: kevin.burns@vuw.ac.nz)

Abstract: Predators can indirectly structure local plant communities by altering the diversity and behaviour of herbivores. These 'trophic cascades' can be seriously disrupted by the local extinction of top predators. They can also be restored by the subsequent re-introduction of top predators by conservationists. Here, we investigated trophic cascades involving kākā, puriri moths and their host trees. New Zealand kākā (*Nestor meridionalis*, Nestoridae) are large parrots that were extirpated from most of its range in the 20th century. Unlike most other parrots, kākā forage primarily by digging through the vascular cambium of trees in search of wood-boring insects. They regularly consume puriri moths (*Aenetus virescens*, Hepialidae), a giant species of ghost moth whose larvae tunnel into the heartwood of trees for protection. Puriri moths are host specific and frequently attack makomako (*Aristotelia serrata*, Elaeocarpaceae), a sub-canopy tree species. We conducted a field experiment in Zealandia, a nature reserve to which kākā were reintroduced over a decade ago, to test the hypothesis that kākā would increase tree fitness by removing larval parasites (i.e. herbivores). Contrary to our expectations, results revealed an additive, negative effect of both the predator (kākā) and parasite (puriri moths) on plant fitness. Therefore, the tri-trophic interactions restored by the reintroduction of kākā into Zealandia appear to be unique, as the actions of the predator decreased fruit and flower production, rather than increasing plant fitness, as typically reported for trophic cascades.

Keywords: herbivory, indirect interactions, New Zealand, parasite, parrot, plant

Introduction

Island ecosystems are dominated by birds, so avian extinctions could have important implications for the functioning of island food webs (Terborgh 2010). For example, seed dispersal networks on islands are smaller and more asymmetric than networks on continents, because many of the birds that once contributed to them are now missing (Schleuning et al. 2014). The subsequent loss of mutualistic function could potentially have cascading effects on seed dispersal and plant recruitment (Wotton & Kelly 2011). Similarly, the local extinction of avian pollinators can lead to pollination failure, lower seed set and reduced recruitment in plants (Anderson et al. 2011).

In addition to direct trophic interactions, indirect effects can also occur among trophic levels in food webs (i.e. 'trophic cascades', Polis et al. 2000; Schmitz et al. 2000; Terborgh & Estes 2013; Ripple et al. 2016). For example, the local extinction of the grey wolf (*Canis lupis*) from Yellowstone Park led to an increase in the abundance of elk (e.g. *Cervus elaphus*), which, in turn, resulted in declines in plant abundances (Ripple & Beschta 2012; Beschta et al. 2018). More recent work in Yellowstone National Park has found that indirect interactions resulting from the reintroduction of top carnivores can also alter the functioning of mutualisms. The local extinction of wolves, and subsequent release of browsing by elk, resulted in reduced availability of fleshy fruits to grizzly bears (*Ursus arctos*; Ripple et al. 2014a).

Oceanic islands are home to some of the most unusual plants and animals on the planet (Burns 2019). Given their isolation, many types of animals that are common on continents fail to disperse to oceanic islands. In their absence, more dispersive species often evolve to take their place ecologically. 'Niche shifts' are commonplace on islands (Diamond 1970, Duthie et al. 2006) and they could conceivably alter the trajectories of trophic cascades that are commonly observed on continents.

Here, we test for indirect effects of insect predation by an avian predator on reproductive effort in a New Zealand tree species. Kākā (*Nestor meridionalis*), large parrots that have been extirpated across most of their former range in New Zealand, forage by digging into trees in search of puriri moths (*Aenetus virescens*), which tunnel into the wood of host trees for protection while they feed off phloem exudate. We conducted a semi-manipulative field experiment to investigate how predation of parasitic moth larvae by kākā might affect flower and fruit production in makomako trees (*Aristotelia serrata*). We compared the fitness of trees with and without parasites, in addition to the fitness of trees with and without kākā predation, in a fully crossed design, to test the hypothesis that kākā predation has a cascading, positive effect on plant fitness.

Methods

Study site & species

Makomako (*Aristotelia serrata*, Eleaocarpaceae) is a common sub-canopy tree species that is endemic to New Zealand. It grows up to 10 m tall, can reach 30 cm in diameter at breast height (DBH) and occurs on all of New Zealand's main islands. It is dioecious, with individual trees being either strictly male or female. Both sexes produce panicles of pink flowers measuring 4–6 mm in diameter. After fertilisation, female trees produce black berries that are approximately 5 × 4 mm long and each contain 8 seeds.

Makomako trees are frequently parasitised by puriri moths (*Aenetus virescens*, Lepidoptera), which are also endemic to New Zealand (Fig 1). Puriri moths belong to the ghost moth family (Hepialidae), and have a wing span of up to 15 cm, making them the largest moth native to New Zealand. Puriri moth larvae begin life on the forest floor, where they consume fungi for several months before ascending suitable host trees. At this stage of their life cycle, they excavate vertical tunnels into the heartwood of host trees, where they live for up to 6 years, emerging at night to feed on tree sap at the tunnel entrance (Grehan & Care 2018). Parasitic larvae spin webs over their feeding scars, which trap heat and increase the foraging efficiency of larvae (Yule & Burns 2017a). Larvae also have strong preferences for specific host species and avoid trees with thick bark (Yule & Burns 2017b). They also infect larger trees more frequently than small trees (Yule & Burns 2015), and male trees have higher parasite loads than female trees (Yule & Burns 2019). Once larvae grow to approximately 10 cm in length, they pupate and emerge from tunnels as moths, which live just long enough to mate and lay eggs (1–2 days).

Puriri moth larvae are the preferred prey of a large, forest-dwelling parrot known as kākā (*Nestor meridionalis*, Strigopoidea). While kākā feed on flowers and fruit, they often forage by digging into trees in search of invertebrate prey that excavate tunnels into wood for shelter. Kākā have a large, downward-arching upper mandible with a sharp tip, which they hook onto tree surfaces. Once their upper mandible is in place, they use their lower mandible to chisel-out thin strips of wood in search of invertebrates. While kākā predation could have a positive effect on tree fitness by removing parasites (i.e. herbivores), alternatively they could also damage the cambium of trees while foraging for puriri moth larvae.
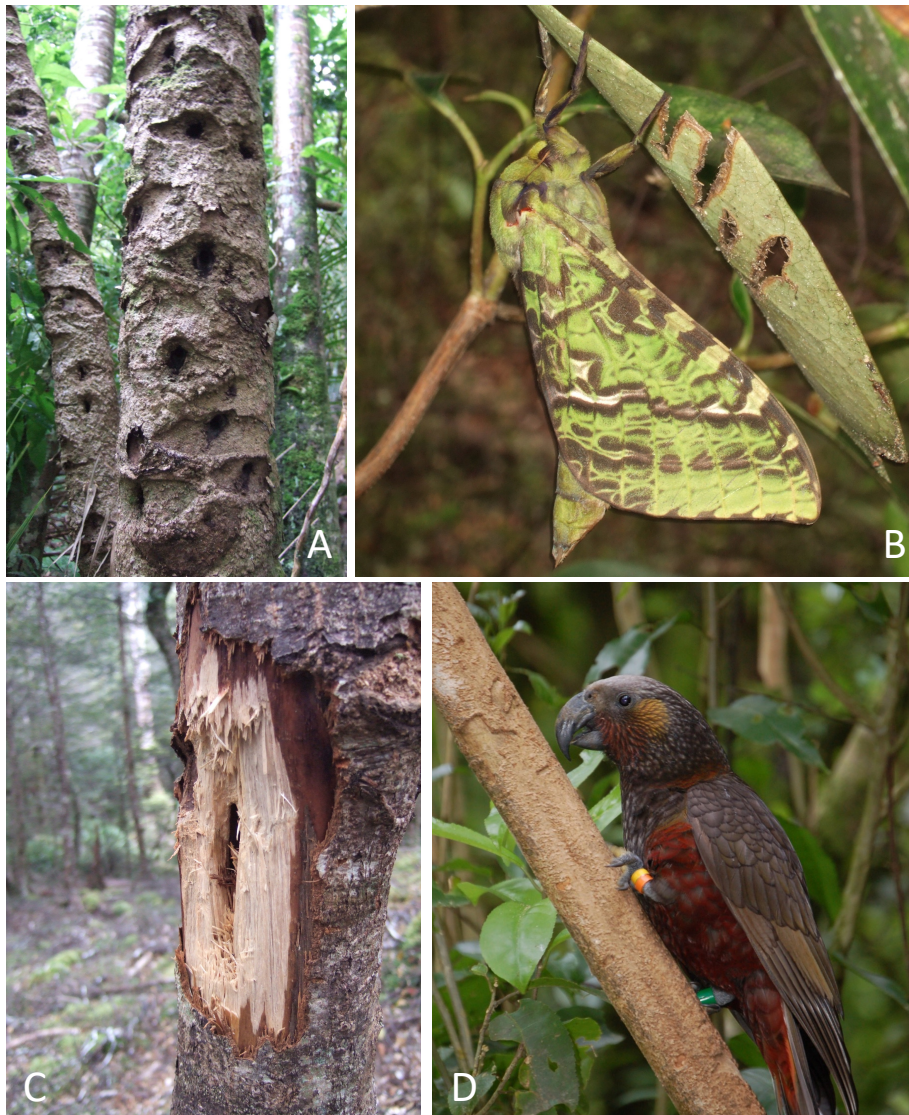

Figure 1. a) Feeding scars on host trees heavily parasitised by puriri moth larvae (*Aenetus virescens*), b) an adult puriri moth, c) damage caused by kākā (*Nestor meridionalis*) foraging for puriri moth larvae, d) an adult kākā.

All data were collected in a forest reserve on New Zealand's North Island known as 'Zealandia' ($41°28'$ S, $174°74'$ W). The reserve was cleared for farming over a century ago, but was abandoned soon thereafter, and it now supports regenerating, mid-successional broadleaf-conifer forest (Blick et al. 2008). Zealandia now houses a large population of makomako host trees, many of which house puriri moth larvae. Kākā were previously extirpated from the region (Moorehouse et al. 2003). However, they were reintroduced into Zealandia in the last decade and are now commonplace (Loepelt et al. 2016).

Experimental design

We hypothesised that predation of puriri moth larvae by kākā has an indirect, positive effect on fruit and flower production in makomako trees (Fig. 2). To test for evidence of this type of trophic cascade, we identified 80 trees at our study site and measured their diameter at breast height (i.e. 1.25 m above the ground). Trees were selected haphazardly, such that half were infected by puriri moths and the other half were free from infection. Of the 40 infected trees, 20 had several parasitic larvae removed by kākā. This facilitated a semi-manipulative experiment with two fully-crossed fixed effects (parasitism
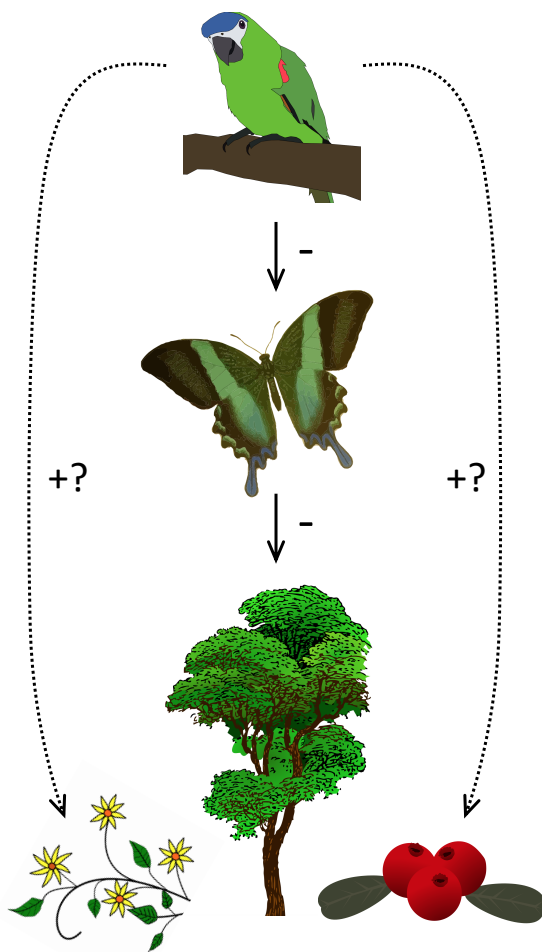

Figure 2. Idealised trophic interactions between parrots, puriri moths and makomako trees. Arrows and symbols refer to the directionality and sign of trophic interactions. Solid arrows indicate direct interactions and dashed lines indicate indirect interactions. We hypothesised that because parrots prey on parasitic lepidopteran larvae, they should have a positive, indirect effect on trees, illustrated as '+?'; however, we observed that parrots decreased flower and fruit production in makomako trees.

and predation), each with two levels (present versus absent). Four treatment combinations were established: (1) free from larval parasites and free from the effects of the predator (n = 20), (2) infected by larval parasites, but free from the effects of the predator (n = 20), (3) free from larval parasites, but affected by the predator (the mechanical action of the predator was simulated by hand, n = 20), (4) both infected by larval parasites and affected by the predator (n = 20).

Kākā only damaged trees that were infected by puriri moths. So for the 'without parasite × with predator' treatment, mechanical damage that was similar to that induced by kākā foraging was simulated by chiselling-out thin strips of wood from non-parasitised trees by hand. Every effort was made to simulate the distinctive effects of kākā foraging. Strips of wood removed by naturally foraging kākā were first collected from the field, measured (66.8 mm ± 2.2 mm long × 6.7 mm ± 1.3 mm wide) and an appropriately-shaped chisel was obtained to remove similarly-shaped strips of wood. To standardise the total amount of surface area affected in the two 'with predator' treatments, the total affected surface area of trees within 2m of the ground was measured using digital photography and software. Kākā damage was simulated such that the affected surface area was similar between treatments affected by kākā ($\bar{x}$ ± SD; un-parasitised = 110.5 cm^2 ± 101.1; parasitised = 154.3 cm^2 ± 236.67). Similarly, the total amount of tree surface area affected by puriri moth larvae between the two 'with parasite' treatments did not differ ($\bar{x}$ ± SD; un-predated = 38.0 cm^2 ± 16.8; predated = 37.3 cm^2 ± 4.4).

Flower and fruit production were assessed over two consecutive fruiting seasons (2015–2016). In each year, the total number of panicles produced by each tree was quantified in ground-based surveys. Five panicles were then randomly selected from each individual, photographed, and the number of flowers per panicle was quantified using ImageJ (Schneider 2012). Total annual flower production was then calculated by multiplying the total number of panicles observed on each tree by the mean number of flowers per panicle, which was then averaged between years. Total annual fruit production was calculated similarly on female trees following flower production.

To investigate how parasites and predators affect flower and fruit production, separate linear models were conducted on different components of plant reproduction. One linear model investigated flower production in both male and female trees, while the other investigated fruit production in just females. Both variables were likely confounded by tree size, as bigger trees typically have higher reproductive output. Flower production might also be confounded by gender, as male plants in dioecious plants typically produce greater quantities of flowers than females (Barrett & Hough 2013).

To explore whether flower production might increase with tree DBH, and whether male trees produced more flowers than female trees, a preliminary general linear model was conducted. The total number of flowers produced by each tree was used as the dependent variable. Sex was considered a fixed factor with two levels and DBH was included as a covariate. Flower number was logarithm-transformed to conform to assumptions. All analyses were conducted in the *R* environment (R Core Team 2015).

Results showed that flower production increased with tree DBH ($t = 7.408$, $p < 0.001$) at similar rates between males and females ($t = -0.453$, $p = 0.652$). However, males consistently produced greater numbers of flowers than females ($t = 10.927$, $p < 0.001$). Similarly, fruit production by female trees,
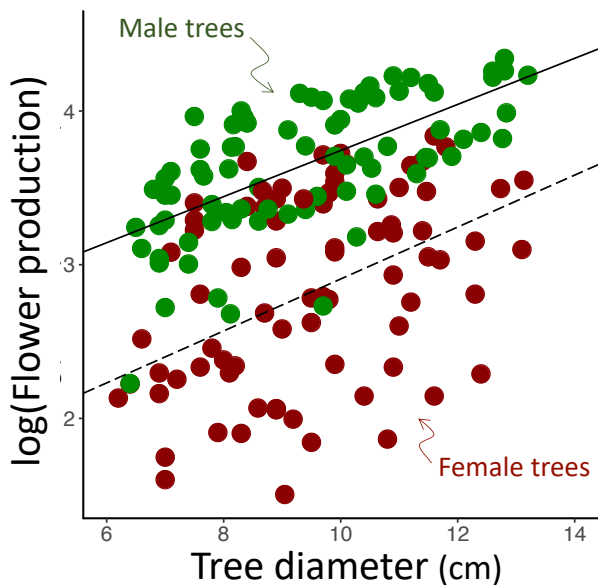
Figure 3. Differences in the relationship between tree size and flower production in male (green symbols, solid line) and female (brown symbols, dashed line) makomako (*Aristotelia serrata*). Although flower production increases with tree diameter at similar rates in both male and female trees, males consistently produce more flowers than females.

logarithm-transformed to conform to assumptions, increased with host DBH ($t = 3.348$, $p = 0.001$). Therefore, both DBH and gender confound analyses of the effect of parasites and predators on flower production (Fig. 3).

To test how parasites and predators affect flower production, a linear model was conducted. The actions of parasites and their predators were considered fixed factors, each with two levels (present vs absent). Gender was also included as a fixed factor with two levels (males vs females) to account for differences in flower production between the sexes. Similarly, tree DBH was included as a covariate to account for the effect of host size on overall reproductive effort.

To test how parasites and predators affect fruit production, a second linear model was conducted. The actions of parasites and their predators were again considered fixed factors, each with two levels. Similar to the previous model, tree DBH was included as a covariate to account for the effect of host size on overall reproductive effort. Because this analysis focused on fruit production, all trees were necessarily female.

Results

Parasitism and predation had an additive effect on flower production in *A. serrata* (Fig. 4a). Parasitism by puriri moth larvae had a negative effect on flower production ($F_{1,154} = 214.947$, $p < 0.001$). However, contrary to our expectations, predation of parasitic larvae by kākā also decreased flower production ($F_{1,154} = 51.414$, $p < 0.001$). Parasitism and predation did not interact ($F_{1,154} = 1.616$, $p = 0.206$). As expected, flower production increased with host DBH ($F_{1,154}$
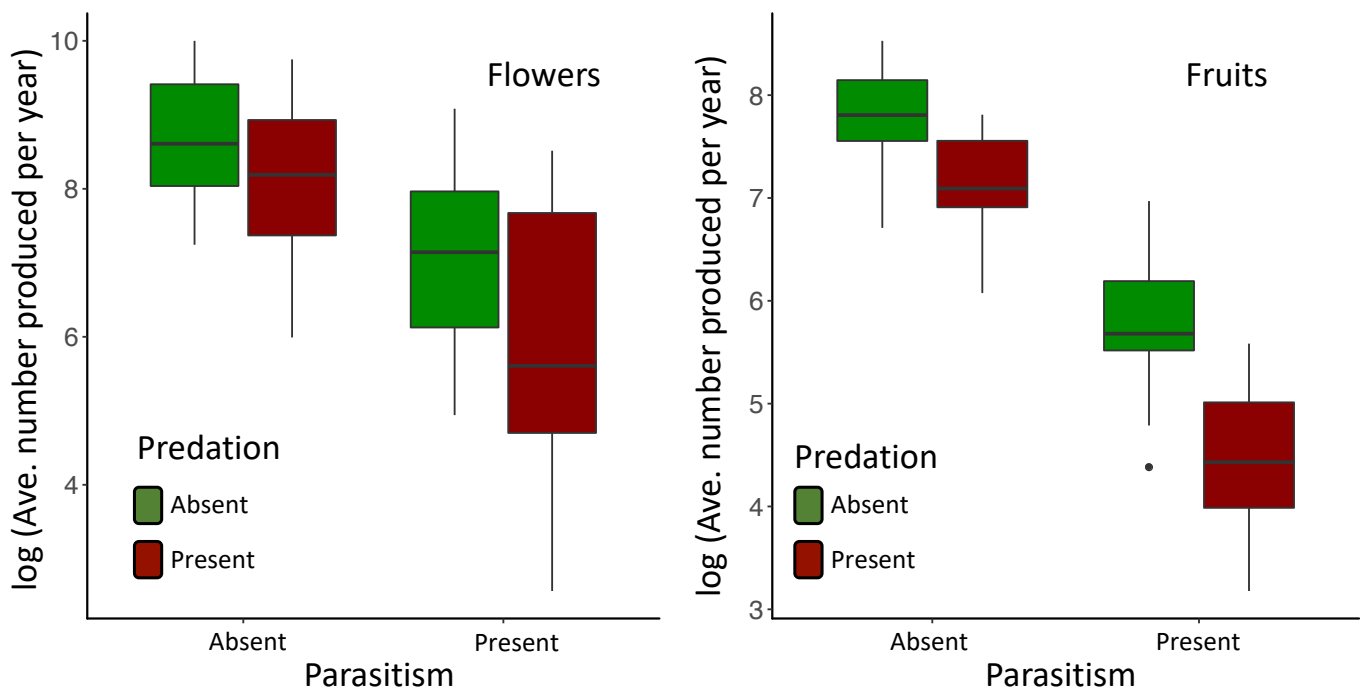

Figure 4. Results from a field experiment investigating how parasitism by puriri moths (*Aenetus virescens*) and their predation by kākā (*Nestor meridionalis*) affects flower and fruit production in makomako (*Aristotelia serrata*), a sub-canopy tree species that is endemic to New Zealand. Boxes represent the interquartile range (IQR) and the horizontal line within the box is the median. Vertical lines extend to the first datapoint that is 1.5 times the IQR. Points are outliers. After controlling for tree diameter and gender, parasitism and predation decreased flower production (left). After controlling for tree diameter, fruit production in female trees also decreased with parasitism and predation (right).

= 139.447, $p < 0.001$) and differed between the sexes ($F_{1,154}$ = 320.944, $p < 0.001$).

Similar results were observed for flower production in females (Fig. 4b). Larval parasitism decreased fruit production ($F_{1,75}$ = 281.150, $p < 0.001$). Predation by kākā also decreased fruit production ($F_{1,75}$ = 54.976, $p < 0.001$). Parasitism and predation did not interact ($F_{1,75}$ = 2.948, p = 0.090). As expected, flower production increased with host DBH ($F_{1,75}$ = 59.494, $p < 0.001$).

Discussion

Over a century ago, Charles Darwin recognised the potential importance of trophic cascades to plant reproduction (Ripple et al. 2016). In the Origin of Species, Darwin (1859) speculated that domesticated cats facilitated the pollination of plants by bees. By predating on mice, who consumed honeycombs produced by bees, cats increased local bee populations, and facilitated the pollination process. Since then, many studies have documented trophic cascades wherein plant biomass increases as a result of the loss of top carnivores (Schmitz et al. 2000, Ripple et al. 2014b). Fewer studies have tested whether the loss of top predators affects flower and fruit production by plants positioned at lower trophic levels. Here, we found that the actions of a top predator can decrease flower and fruit production by plants.

This result is inconsistent with most previous work on trophic cascades. For example, in the absence of tiger sharks (*Galeocerdo cuvier*), herbivory by sea cows (*Dugong dugon*) and sea turtles (*Chelonia mydas*) increases, altering the structure and function of sea grass beds (*Cymodocea* spp. and *Halodule* spp.) in Western Australia (Burkholder et al. 2013). Ripple et al. (2014a) showed that in the absence of wolves, elk numbers increased in Yellowstone National Park and supressed fruit production in serviceberry (*Amelanchier alnifolia*, Rosaceae), a favoured food of grizzly bears. Wang et al. (2018) found that predatory ants (*Oecophylla smaragdina*) lower the abundance of non-pollinating, parasitic wasps (*Sycophaga mayri*), leading to increased seed set in figs (*Ficus racemosa*). Taken collectively, these studies demonstrate that the extinction of apex predators from food webs can not only affect the biomass of plants, but also ecological interactions between species at lower trophic levels.

Trophic cascades typically involve positive indirect effects been predators and plants (Sipura 1999, Mooney et al. 2010). However, the strength and sign of indirect interactions can differ between food webs (Casey et al. 2017) and habitats (see Trussell et al. 2006). Results reported here add to a growing body of literature illustrating that a broader range of tri-trophic interactions are possible (Schmitz et al. 2004).

Woodpeckers are absent from most of Australasia and Oceania, and in their absence, kākā seem to have evolved to replace them ecologically as predators of wood-boring arthropods in New Zealand. Although woodpeckers can damage trees as they drill for insects, kākā forage differently to obtain wood-boring insects. They use their larger, upper mandible as an anchor and chisel-out thin sections of wood using their broad, bevel-shaped lower mandible, which appears to cause extensive damage the vascular cambium of trees.

Makomako trees rely on animal mutualists for pollination and seed dispersal. Their flowers are pollinated mostly by insects, while their fleshy fruits are consumed mostly by birds (O'Donnell & Dilks 1994; Burns 2013). Therefore, negative tri-trophic interactions observed here lower resource availability to pollinators and seed dispersers, which could conceivably affect plant recruitment (see Anderson et al. 2011).

Given that kākā have been exterminated across most of their former range, we predicted at the outset of this study that their re-introduction into nature reserves would have positive effects on the fitness of makomako trees. However, contrary to our predictions, we found that predatory kākā actually decreases flower and fruit production, presumably because of their unusual and somewhat destructive foraging method. The tri-trophic interactions observed in this insular food web therefore appear to operate differently than a trophic cascade, which we hypothesised based on prior knowledge of the system. Additional work on other tri-trophic interactions in New Zealand is needed to determine whether insular food webs consistently function differently to those on continents (Terborgh 2010).

Acknowledgements

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