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RESEARCH

Seasonality and dietary diversity in flower and fruit consumption by birds: long-term dataset from a New Zealand wildlife reserve

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Abstract: Seasonal dynamics shape the timing and intensity of bird-plant interactions but are increasingly altered due to anthropogenic disturbances such as biodiversity loss and climate change. Baseline data on these patterns are critical, especially for restored communities where threatened bird species act as both pollinators and seed dispersers. We documented bird-plant interactions in Zealandia ecosanctuary, New Zealand, over nine years and investigated seasonal patterns in the timing, duration, and rate of avian visits to flowers and fruits at both the community and individual plant species levels. Additionally, we compared the dietary diversity of the avian community and the evenness with which different species consumed flowers and fruits. During 568 hours of sampling between 2006 and 2015, we observed 1327 flower visits and 2886 fruit visits involving eight native bird species and 25 native plant species. Flower visitation peaked in October (austral spring), while fruit visitation peaked in April (austral autumn). Seven bird species visited the flowers of ten plant species, with *Fuchsia excorticata* having the highest visitation rate (16.4 visits per hour). Eight bird species consumed the fruit of 20 plant species, with *Coprosma robusta* (8.6 visits per hour) and *Geniostoma ligustrifolium* (8.1 visits per hour) being the most visited. Visits were temporally staggered among plant species for both flowers and fruits. Fruits that were visited mid-season and flowers with high visitation rates had the broadest temporal spreads of visits. Fruits had a more even distribution of visits than flowers, indicating a broad exploitation of fruit resources compared to a more specialised use of floral resources. Our findings reveal strong seasonal partitioning of bird-plant interactions, with distinct and staggered peaks in flower and fruit visitation that likely reflect resource availability. This seasonal partitioning indicates that birds track seasonal resource shifts to sustain year-round foraging. These results provide long-term baseline data for a restored community of threatened mutualists, offering a reference point for detecting and managing future shifts under environmental change.

Keywords: bird-plant interactions, dual mutualisms, frugivory, long-term dataset, nectivory, New Zealand, seasonality

Introduction

The arrival of humans in New Zealand caused severe declines in the endemic avifauna due to over-hunting, predation by mammalian pests, and habitat loss (Craig et al. 2000; Innes et al. 2022). Consequently, many forest birds became extinct globally, such as moa (Dinornithiformes), piopio (*Turnagra* spp.), and huia (*Heteralocha acutirostris*) (Holdaway 1989). Others like hihi (*Notiomystis cincta*) and tīeke (*Philesturnus* spp.) died out on the main islands, and relict populations remained only on a few predator-free offshore islands (Castro et al. 2003; Hooson & Jamieson 2003). These changes in forest community composition altered ecological processes, such as bird-plant mutualisms (Burns 2013a). Recent conservation efforts, such as pest management, habitat restoration, and translocations to fenced sanctuaries like Zealandia Te Māra a Tāne (henceforth referred to as Zealandia) in Wellington city, have partially restored some forest bird communities on New Zealand's main islands (Howald et al. 2007; Miskelly & Powlesland 2013; Innes et al. 2019). Understanding how these recovering bird communities interact with native plants is critical for assessing restoration success and anticipating future changes in ecosystem function.

Many plants rely on birds for mutualistic interactions such as pollination and seed dispersal. Correspondingly, many groups of birds have evolved traits to facilitate such mutualistic interactions. For instance, hummingbirds (Trochilidae) and sunbirds (Nectariniidae) are specialist pollinators that feed almost entirely on nectar (Abrahamczyk 2019), while frugivorous birds, such as toucans (Piciformes) and hornbills (Bucerotiformes), play a vital role as seed dispersers in tropical forests (Kitamura et al. 2011; Naniwadekar et al. 2015, 2019; Corlett 2021). In New Zealand, forest birds such as tūī (*Prosthemadera novaeseelandiae*), korimako | bellbird (*Anthornis melanura*), and pōpokotea | whitehead (*Mohoua albicilla*), are often dual mutualists, acting as both

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pollinators and seed dispersers for native plants (Clout & Hay 1989; Kelly et al. 2010; Burns 2013a; Fuster et al. 2019; Lim & Burns 2023). Consequently, these birds feed on different plant resources from season to season (O'Donnell & Dilks 1994; Scott et al. 2003; Kelly et al. 2010). O'Donnell and Dilks (1994) studied the habitat use and foraging ecology of the avian community in South Westland in the South Island of New Zealand. Eighteen species of omnivorous birds exhibited sequential dietary specialisation to varying levels as they switched seasonally between different food resources (O'Donnell & Dilks 1994). No equivalent long-term study has been published for the North Island, or in restored habitats for recovering bird communities.

In seasonal habitats, the temporal availability of plant resources (e.g. flower and fruit production) corresponds to the seasonally changing nutritional demands of their consumers (e.g. pollinators and seed dispersers) (Snow & Snow 1971; Herrera 1982). These bird-plant interactions may represent true coevolved mutualisms (Stiles 1985). Previous studies on seasonality in species interactions have provided key insights into mutualistic networks under various ecological contexts. For instance, in a subtropical forest in Costa Rica, seasonal flower visitation by 22 hummingbird species enabled the partitioning of the avian community into sub-communities defined by their distinct seasonal trends in flower visitation, thereby reducing interspecific competition and highlighting the role of temporal complementarity in maintaining biodiversity and ecosystem functioning (Stiles 1985). In the humid tropical forests of Trinidad (Snow 1965) and temperate forests of southern England (Snow & Snow 1988), where birds are predominantly seed dispersers, fruits of at least a few plant species were available to birds year-round, facilitating fruit consumption by birds throughout the year. On Vancouver Island in British Columbia, Burns (2002) reported that plants producing fruits earlier in the season had higher fruit removal rates, which may facilitate increased phenological synchrony between plants and birds by selecting for earlier dates of fruit maturation. These examples illustrate how seasonal dynamics of bird-plant interactions vary across ecological contexts, emphasising the need to understand such patterns in recovering temperate forest communities like those in New Zealand.

Climate change continues to alter the timing and duration of cyclical seasonal events like flowering and fruiting across ecosystems worldwide (Parmesan 2006; Cleland et al. 2007; Inouye 2022). Shifts in temperature and precipitation regimes disrupt the phenological synchrony between plants and their avian mutualists, potentially affecting pollination and seed dispersal success (Memmott et al. 2007; Renner & Zohner 2018; Duchenne et al. 2021). In New Zealand, however, there remains considerable uncertainty about biodiversity responses to both direct and indirect threats posed by climate change (McGlone et al. 2010; Lundquist et al. 2011; Macinnis-Ng et al. 2021). Establishing current baselines of temporal trends in bird-plant interactions is therefore essential for detecting and predicting the impacts of environmental change on the seasonal timing of such interactions.

The recovering bird community at Zealandia offers a unique opportunity to investigate seasonal patterns of community-level resource use within a regenerating North Island forest where introduced predators are excluded and with a reintroduced avian community. We documented bird-flower and bird-fruit interactions in Zealandia over nine years and compiled a comprehensive dataset to investigate seasonal trends in flower and fruit visitation. We quantified these interactions using the related parameters of the time of occurrence (mean), duration (range), and synchrony (variance) (Rathcke & Lacey 1985). Because New Zealand birds interact with plants as both nectivores and frugivores, we compared visitation patterns between flowers and fruits to reveal complementary or contrasting strategies of resource use.

We investigated seasonal variation in bird visitation to flowers and fruits by analysing the timing of peak visits and the temporal spread of visitation at both the community and individual plant species levels, pooling the data across all sampling years and bird species. We tested the hypothesis that native forest birds, as dual mutualists, exhibit distinct and temporally separated flower and fruit visiting seasons, with visits to individual plant species staggered within these seasons. We then used the pooled data to examine how visitation patterns, specifically peak timing, temporal spread of visitation, and visitation rates at the individual plant species level contribute to broader seasonal trends. The mid-domain effect suggests that randomly distributed periods of resource availability tend to converge most frequently during the middle of the season (Morales et al. 2005; Letten et al. 2013; Du et al. 2024). If the timing of peak visits by birds reflects the seasonal availability of plant resources, we predict that flowers and fruits visited near the middle of the season will have a broader temporal spread of visits due to overlapping resource availability, while those peaking near the season's start or end will have a narrower temporal spread of visits. If resource availability earlier in the season is advantageous for mutualistic interactions (Burns 2002), we predict that plant species flowering and fruiting earlier in their respective seasons will have higher visitation rates. Furthermore, if abundant resources sustain repeated visitation over longer periods (Fowler et al. 2016), we predict that plant species with a greater temporal spread of visits will have higher visitation rates. Lastly, we pooled the data across all years and plant species to assess the dietary diversity of bird species and the relative evenness with which they consume flower versus fruit resources. We predicted greater diversity and evenness in the fruit species visited compared to flower species, since birds visit a higher number of plant species for fruit resources than floral resources (Kelly et al. 2010; Burns 2013a). We have published the long-term dataset on bird-flower and bird-fruit visitation in its entirety, in the hope of facilitating future work.

Methods

Study site

All data were collected in Zealandia (41°18′3″ S, 174°44′8″ E), a wildlife reserve located in Wellington on the southern tip of the North Island of New Zealand. Zealandia is surrounded by an 8.6 km-long perimeter fence designed to exclude all introduced mammalian pests except for mice (*Mus musculus*) (Blick et al. 2008). Situated 160–380 m above sea level, the reserve experiences a mild, temperate climate, and receives around 127 cm of rainfall annually. Many threatened bird species have been translocated within the reserve, including the previously locally extinct pōpokotea, korimako, and tīeke | North Island saddleback (*Philesturnus rufusater*) (Miskelly et al. 2005). Kākā (*Nestor meridionalis*) and kererū | New Zealand pigeon (*Hemiphaga novaeseelandiae*), both large frugivores, have also been reintroduced. The critically endangered hihi | stitchbird (*Notiomystis cincta*) was translocated to the sanctuary in 2005, marking the first time this species was present on mainland

New Zealand in 150 years (Miskelly 2018). The populations of tūī and tauhou | silvereye (*Zosterops lateralis*) that were already present in low numbers before the fence installation were greatly increased as a result of the pest eradication and exclusion (Bell 2015). Bird populations within the reserve and in surrounding areas are increasing due to ongoing pest eradication and habitat management (McArthur et al. 2024).

Data collection

Field observations were carried out over nine years between 2006 and 2015. Sampling was conducted approximately once every five days from January 2006 to December 2011, and then less frequently from January 2012 to April 2015, approximately once every nine days. We quantified bird-flower and bird-fruit visits by observing wild birds foraging along a 4.6 km trail that took approximately 1 hour to traverse. Observations were conducted between 11:00 and 14:00 hours and discontinued if interrupted by heavy rains or wind. Wild birds moved erratically through the dense foliage, making it difficult to accurately estimate the exact number of foraging interactions. Thus, interactions were quantified more generally, following Snow & Snow (1988) and Burns (2006). A visit was scored when a bird was seen feeding from at least one flower or eating at least one fruit. Observations ceased after each recorded visit and resumed approximately 10 m down the trail to avoid counting the same bird-plant interaction more than once. We only included interactions between native birds and plants, although introduced bird and plant species were also observed occasionally (Burns 2012). The full dataset may be found in the online supplementary material (Appendices S1–S4). Bird and plant species with fewer than three recorded interactions per food resource were excluded from further analyses. For instance, flowers of māhoe (*Melicytus ramiflorus*) were visited only once by a korimako, and hence this interaction was excluded from the analyses. Kākāriki | red-crowned parakeet (*Cyanoramphus novaezelandiae*) were reintroduced to Zealandia close to the beginning of the observation period, so were present in low numbers in the reserve. Kākāriki were observed twice visiting fruits of kanono (*Coprosma grandifolia*) and once visiting fruits of makomako (*Aristotelia serrata*) over the study period and so these records were also excluded from the analyses.

Statistical analyses

To examine whether the timing of flower and fruit visitation varied seasonally, we pooled the flower and fruit visitation records from all bird and plant species over all sampling years and analysed the data using circular statistics (Berens 2009), given that time is a non-linear variable. A circle represented one cycle (i.e. one calendar year), and we analysed the timing of visitation within this cycle (see Jammalamadaka & Sengupta 2001). Each calendar month was first assigned a corresponding numerical value (e.g. January = 1, February = 2, ..., December = 12), with visitation counts recorded as the frequency of each value. These were then converted to angular data by multiplying by 30, placing each month at 30° intervals around the circle (360°/12). This approach standardised months regardless of their varying number of days (Pewsey et al. 2013). The corresponding frequencies of flower and fruit visitation were then represented as angular data in degrees and used to calculate circular statistics. Seasonality of visitation was visualised using circular frequency distributions containing 12 bins, one for each month, going clockwise from January.

For both resources, we calculated two parameters using the angular data to summarise the annual distribution of visits: (1) circular mean ($\bar{\Theta}$ in degrees): a measure of central tendency to identify the timing of peak visits, and (2) circular standard deviation (csd in degrees): a measure of the spread of visits around the peak. A smaller circular mean indicates peak visitation earlier in the calendar year, and a larger circular mean indicates peak visitation later in the calendar year, corresponding to the angular values assigned for each month. Likewise, a smaller circular standard deviation indicates a narrower temporal spread of visits, while a larger circular standard deviation suggests a broader temporal spread of visits around the circular mean (see Wright & Calderon 1995; Ting et al. 2008, Menon et al. 2024). We assessed the annual distribution of visits to each resource using Rayleigh's test of uniformity ($\alpha = 0.05$), which tests the null hypothesis that the circular data is uniformly distributed throughout the year (Pewsey et al. 2013). We also tested for similarity between the seasonal timing of flower and fruit visits using Mardia-Watson-Wheeler's test for homogeneity ($\alpha = 0.05$) (Jammalamadaka & Sengupta 2001; Pewsey et al. 2013). This non-parametric test comparing circular distributions was used instead of the Watson-William's test for homogeneity of means since our data did not meet the assumption of a high concentration parameter required for the Watson-William's test (Pewsey et al. 2013; Landler et al. 2021). Sampling effort was more standardised for the first six years of sampling (2006–2011), compared to the remaining sampling duration (2012–2015). Thus, we repeated the above analyses on the subset of the data that was collected between 2006 and 2011 to assess whether seasonal patterns were affected by differences in sampling effort.

We calculated the circular means and circular standard deviations of visitation for each plant species separately across all sampling years and bird species. Additionally, we determined the visitation rates, or the number of visits per sampling hour, for flower and fruit resources for each plant species across all sampling years and bird species. The sampling effort was not consistent for all months in the study period, so we calculated visitation rates by dividing the sum of recorded visits in each calendar month by the total number of hours sampled for the calendar month over the entire study duration. We compared the circular distributions of visits to each pair of plant species using the Mardia-Watson-Wheeler's test to assess whether flower and fruit visits were temporally staggered between plant species throughout the year.

To examine whether the seasonality of visits to individual plant species influenced overall temporal patterns of flower and fruit visitation, we quantified pairwise relationships between the timing of peak visits (circular mean), temporal spread of visits (circular standard deviations), and visitation rates (number of visits per sampling hour). To test the hypothesis that plants visited in the middle of the flowering or fruiting season would be visited for a longer duration, we evaluated the fit of a sinusoidal curve of the circular means and circular standard deviations for each plant species. To test whether visitation rates varied linearly with the circular means and circular standard deviations for flower and fruit resources, we used a series of linear regressions.

Finally, we compared the visitation diversity and evenness for each bird species between flower and fruit resources. For both resource types, visitation diversity was quantified using the Shannon diversity index (Shannon 1948), which measures both the number of plant species visited and the relative frequency of visits to each species. Visitation evenness among plant species was assessed using Pielou's evenness index

(Pielou 1966), which measures the uniformity of visitation across species, with values approaching 1 indicating that visits were distributed more evenly among available plant species. Differences in visitation diversity and evenness between flower and fruit resources were tested using Wilcoxon rank sum tests.

To assess the influence of sampling effort on the observed interactions, we plotted sampling accumulation curves for cumulative unique interactions recorded over the study duration and examined sampling completeness using Chao1 asymptotic richness estimates (Chao 1987). Additionally, as sampling effort was inconsistent between months, we plotted the sampling accumulation curves for each calendar month separately and examined sampling completeness using Chao1 asymptotic richness estimates for each calendar month (Chao 1987). All analyses and visualisations were conducted in the R environment using the "circular", "ggplot2", and "vegan" packages (Wickham 2016; Agostinelli & Lund 2022; Oksanen et al. 2022; R Core Team 2022).

Results

Between 2006 and 2015, a total of 4213 feeding visits (1327 flower visits and 2886 fruit visits) were observed over 568 hours of sampling (Appendix S1). Eight species of native birds, tūī, tauhou, korimako, kererū, hihi, kākā, tīēke, and pōpokotea, visited 25 native plants during the study (Table 1). The timing of flower and fruit visitation by birds varied throughout the year. Flower visitation was higher between August and December, peaking in late October ($\bar{\theta}$ = 290 ± 56°; Fig. 1a). Fruit visitation was higher between February and June, peaking in late April ($\bar{\theta}$ = 118 ± 57°; Fig. 1b). Visitation followed a unimodal distribution for both flower ($Z = 0.161$, $p = 0.002$) and fruit ($Z = 0.198$, $p < 0.001$) visits, indicating significant seasonal peaks in the consumption of both resources. Circular distributions of visitation differed significantly between fruit and flower visits throughout the year ($W = 403.79$, $p < 0.001$), indicating that the seasonal distributions of flower and fruit visits were temporally distinct.

Visits to flowers of ten native plant species (Fig. 1c) and fruits of 20 native plant species (Fig. 1d) were observed during the study. Five plant species were visited for both flowers and fruits: *Fuchsia excorticata*, *Geniostoma ligustrifolium*, *Pseudopanax arboreus*, *Pittosporum eugenioides*, and *Schefflera digitata* (Burns 2013a). *Fuchsia excorticata* flowers had the highest visitation rate (16 visits per hour of sampling), followed by flowers of *Phormium tenax* (5 visits per hour), *P. arboreus* (4 visits per hour), and *Sophora microphylla* (3 visits per hour). *Coprosma robusta* fruits had the highest visitation rate (9 visits per hour).

Table 1. Summary of flower and fruit visitation for all bird species combined, sampled from Zealandia ecosanctuary in Wellington, New Zealand, between 2006 and 2015. Visitation records were pooled across all sampling years and all bird species. Codes in parentheses in the first column are used in figures 2 and 3 and correspond to plant species names. Visitation rates (number of visits per hour, column 'rate'), timing of peak visits or circular mean (column '$\bar{\theta}$', in degrees), and temporal spread of visits or circular standard deviations (column 'csd', in degrees) are indicated for flower and fruit resources. A higher circular mean indicates a later date of peaks in visits and higher circular standard deviations indicate a broader temporal spread of visits. Cells with dashes indicate that no interactions were observed for that plant species.

Plant species (code)	**Flower**			**Fruit**		
	rate	**$\bar{\theta}$**	**csd**	**rate**	**$\bar{\theta}$**	**csd**
Aristotelia serrata (AS)	-	-	-	0.68	52.8	14.4
Coprosma grandifolia (CG)	-	-	-	4.26	76.8	32.3
Coprosma robusta (CR)	-	-	-	8.57	150.1	48.5
Coriaria arborea (CA)	-	-	-	1.9	70.7	64.3
Elaeocarpus dentatus (ED)	-	-	-	0.29	114.7	56.9
Fuchsia excorticata (FE)	16.39	277.7	45.8	1.02	25.9	32.4
Geniostoma ligustrifolium (GL)	0.69	302.6	8.6	8.06	144.8	24.8
Hedycarya arborea (HA)	-	-	-	0.56	44.9	32.9
Hoheria sexstylosa (HS)	0.19	92.9	8.9	-	-	-
Knightia excelsa (KE)	0.19	330.0	0.00	-	-	-
Melicytus ramiflorus (MR)	-	-	-	7.62	97.6	39.9
Metrosideros excelsa (ME)	0.09	35.9	11.99	-	-	-
Muehlenbeckia australis (MA)	-	-	-	0.95	148.7	20.6
Myoporum laetum (ML)	-	-	-	2.35	133.2	30.3
Myrsine australis (MyA)	-	-	-	3.59	79.0	71.6
Phormium tenax (PT)	5.07	353.0	19.7	-	-	-
Piper excelsum (PEx)	-	-	-	1.46	77.6	25.7
Pittosporum eugenioides (PE)	0.15	300.0	0.00	2.36	181.9	28.8
Pittosporum tenuifolium (PTe)	-	-	-	0.23	180.0	19.0
Podocarpus totara (PTo)	-	-	-	0.77	143.0	20.1
Pseudopanax arboreus (PA)	4.11	231.7	22.3	7.02	94.9	49.7
Ripogonum scandens (RS)	-	-	-	0.26	99.2	72.6
Rubus cissoides (RC)	-	-	-	0.23	42.8	14.9
Schefflera digitata (SD)	0.4	54.9	30.9	6.19	162.2	31.8
Sophora microphylla (SM)	3.11	290.7	16.3	-	-	-

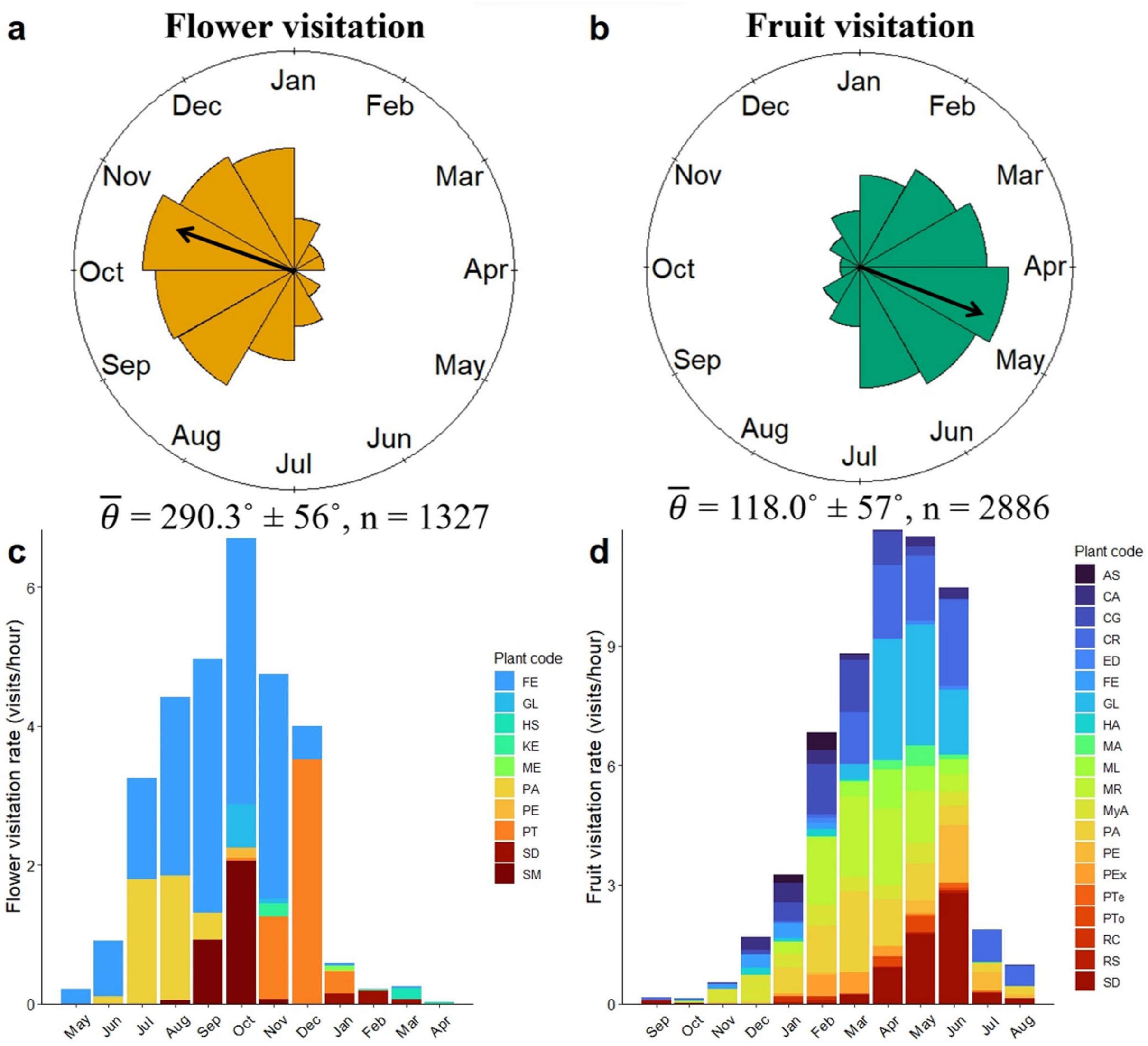

Figure 1. Seasonality of bird-flower and bird-fruit visitation sampled from Zealandia ecosanctuary in Wellington, New Zealand, between 2006 and 2015. Visitation records were pooled across all sampling years and all bird species. Each segment in the circular histograms represents one calendar month and occupies 30˚ of the circle. The size of each segment represents the relative proportion of visits recorded in each month. Black arrows indicate the circular mean (timing of peak visits) for flowers (a) and fruit (b), with longer arrows representing a lower temporal spread of visits. Each segment in the stacked bar plots represents the visitation rate (number of visits per hour) for flowers (c) and fruit (d) of each plant species per month. Refer to Table 1 for plant species names corresponding to the codes in the legend.

Visitation to both flowers and fruits by birds was temporally staggered among plant species. For example, visits to *P. arboreus* flowers peaked earlier in the season, followed by visits to the flowers of *S. microphylla* and *P. tenax.* Likewise, visits to *C. grandifolia* fruits peaked earlier in the season, followed by visits to the fruits of *P. arboreus*, *M. ramiflorus*, and *C. robusta*. Pairwise comparisons of the seasonal distributions of visits between plant species showed that visits to both flowers and fruits were temporally distinct for most pairs ($p < 0.05$, Mardia-Watson-Wheeler's test with Bonferroni correction), with some exceptions (Appendix S2). Flower visits to two species pairs, *G. ligustrifolium* and *P. eugenioides*, and *Metrosideros excelsa* and *S. digitata*, had similar seasonal distributions ($p > 0.05$, Mardia-Watson-Wheeler's test with Bonferroni correction). Fruit visits to ten species pairs, *C. robusta* and *Elaeocarpus dentatus*, *Coriaria arborea* and *Hedycarya arborea*, *C. arborea* and *Ripogonum scandens*, *E. dentatus* and *Myrsine australis*, *E. dentatus* and *S. digitata*, *F. excorticata* and *H. arborea*, *G. ligustrifolium* and *Podocarpus totara*, *Muehlenbeckia australis* and *P. totara*, *Myrsine australis* and *R. scandens*, and *P. eugenioides* and *Pittosporum tenuifolium*, had similar seasonal distributions ($p > 0.05$, Mardia-Watson-Wheeler's test with Bonferroni correction).

To account for the variation in sampling effort between 2006–2011 and later years, we analysed the subset of data between January 2006 and December 2011 in isolation. This analysis yielded similar results to that of the full dataset. A total of 3536 feeding visits (1022 flower visits and 2514 fruit visits) were observed over 435 hours of sampling in the data subset. Flower visitation peaked in late October ($\bar{\Theta}$= 292 ± 54°) and fruit visitation was highest between February and June, peaking in early May ($\bar{\Theta}$= 126 ± 56°). Flowers of nine native plant species and fruits of 20 native plant species were visited. Flowers of *P. eugenioides* were not visited during this period, making this the only species from the full dataset not included in the subset of the data. Visitation again followed a unimodal distribution throughout the year for both flowers ($Z = 0.6367$, $p < 0.001$) and fruits ($Z = 0.6202$, $p < 0.001$), and visits to flowers and fruits peaked at opposite times of the year ($W = 299.61$, $p < 0.001$). The similar results for distributions of visits for the subset of the data compared to the full dataset indicate that the observed seasonal patterns in flower and fruit visits were likely not affected by differences in sampling effort.

Pairwise relationships between plant species-level timing of peak visits (circular mean), temporal spread of visits (circular standard deviation), and visitation rate yielded two significant relationships (Appendix S3). For flower visits, there was no relationship between circular means and circular standard deviations ($R^2 = -0.124$, $p = 0.932$; Fig. 2a), whereas the circular means and circular standard deviations for fruit visits followed a sinusoidal distribution ($R^2 = 0.203$, $p < 0.05$; Fig. 2b), consistent with our predictions of a mid-domain effect. Thus, plant species whose fruits were visited near the beginning or end of the fruiting season were visited over a shorter period, while those whose fruits were visited around the middle of the fruiting season had a higher temporal spread of visitation. Circular means and visitation rates for flower ($R^2 = 0.186$, $p = 0.119$; Fig. 2c) and fruit visits ($R^2 = 1.385$, $p = 0.255$; Fig. 2d) did not vary significantly in a linear manner, contrary to our prediction of a positive relationship between peak timing and rate of visits. Flower visitation rate increased linearly with circular standard deviation ($R^2 = 0.477$, $p < 0.05$; Fig. 2e), indicating that flowers of plant species that were visited at a higher rate also had a higher temporal spread of visitation. To test whether this pattern was driven by *F. excorticata*, we repeated the analysis excluding this species, and the relationship was no longer significant ($R^2 = 0.224$, $p = 0.112$). No relationship was detected between fruit visitation rate and circular standard deviations of fruit visits ($R^2 = -0.015$, $p = 0.407$; Fig. 2f).

Birds visited twice as many fruit species as flower species. Of the eight bird species, tūī ($n = 18$) and tauhou ($n = 17$) visited the highest number of fruit species, followed by hihi ($n = 14$) and tīeke ($n = 14$). Kererū visited the lowest number of fruit species ($n = 6$). Tūī ($n = 10$) visited the highest number of flower species, followed by hihi ($n = 6$) and tauhou ($n = 5$). Tīeke visited the lowest number of flower species ($n = 2$), while kererū were not observed visiting flowers (see Lim & Burns 2023). Visitation diversity and evenness were both significantly higher for fruits than for flowers ($W = 1$, $p < 0.001$ and $W = 8$, $p < 0.05$, respectively; Fig. 3).

Sampling effort was greater during the fruiting season (January–June; 318 hours) than the flowering season (July–December; 250 hours). According to the Chao1 asymptotic richness estimator, our sampling captured 93% of all estimated bird–flower interactions and 90% of bird–fruit interactions for the entire study duration, indicating a high degree of overall sampling completeness (Appendix S4). However, interaction accumulation curves for each calendar month suggested that reduced effort during certain months over the study period may have led to some interactions being missed (Appendix S4). Sampling completeness was highest in August (94%), January (85%), and July (80%), whereas it was lowest in November (33%), suggesting that some interactions may have gone undetected during this month (Appendix S4).

Discussion

Our findings revealed distinct flower and fruit visitation seasons by the forest bird community in Zealandia, consistent with earlier accounts of seasonal resource switching by New Zealand birds (O'Donnell & Dilks 1994). Because most breeding forest birds in New Zealand are sedentary and territorial rather than long-distance migrants (Diamond 1984; Burns 2013b), they must rely on local and seasonally available resources throughout the year (O'Donnell & Dilks 1994; Innes et al. 2022). Flower visits peaked in mid-spring, while fruit visits peaked during autumn, likely corresponding to the seasonal availability of plant resources. Moreover, flower and fruit visits were temporally staggered among plant species within the respective seasons. This contrasts with the year-round fruit visitation by seed dispersers in the forests of Trinidad (Snow 1965) and southern England (Snow & Snow 1988), where fruit availability is temporally staggered between plant species throughout the year. The observed temporal patterns likely reflect coevolution between plants and birds, which may help explain the high prevalence of dual-mutualist species in New Zealand (Stiles 1985; Kelly et al. 2010; Burns 2013a) and align with the generally greater occurrence of dual mutualists on islands (Fuster et al. 2019).

Within-community temporal partitioning of resource availability among plant species may reduce interspecific competition for pollinators and seed dispersers, align with fruit maturation schedules, or reflect species-specific physiological responses to environmental factors such as light, moisture, and temperature (Primack 1985; Stephens et al. 2022). The observed temporal staggering of flower and fruit visits by birds supports this potential phenological partitioning. For example, *P. arboreus* produces flowers from June to August, *S. microphylla* from August to October, and *P. tenax* from September to January (de Lange 2025d, 2025e), which aligns closely with the visitation peaks observed in our study: *P. arboreus* in August, *S. microphylla* in October, and *P. tenax* in December. Similarly, *C. grandifolia* produces fruit from September to April, *M. ramiflorus* from November to March, and *G. ligustrifolium* from March to July (de Lange 2025a, 2025b, 2025c, 2025g), which corresponds with their observed visitation peaks: *C. grandifolia* in March, *M. ramiflorus* in March–April, and *G. ligustrifolium* in May. However, *S. digitata* typically produces fruit in February–March (de Lange 2025f), whereas in our study, visits to *S. digitata* fruit peaked in June. This discrepancy may be caused due to differences in plant phenology in response to microhabitat variability between different locations (Olliff-Yang & Ackerley 2020; Beck & Givnish 2021; Kim & Oh 2025). Documenting the flowering and fruiting phenology of plants alongside visitation records would help account for habitat-specific variation and resolve the relationship between resource availability and use by birds.

Fruit visitation showed strong evidence for the mid-domain effect (Morales et al. 2005; Du et al. 2024), with peak fruit visits to most plant species occurring during the middle of the season. This may reflect more stable climatic conditions during this period, facilitating extended fruit availability. Flower visitation, however, showed no such trend, suggesting a lower degree of overlap between flower visits to different plant species. Unlike *F. excorticata*, plants such as *P. arboreus*, *S. microphylla*, *P. tenax*, and *S. digitata* had short and temporally distinct windows of flower visitation. Therefore, the seasonal dynamics of flower visitation were likely characterised by strong temporal partitioning and potential competition for nectivores among

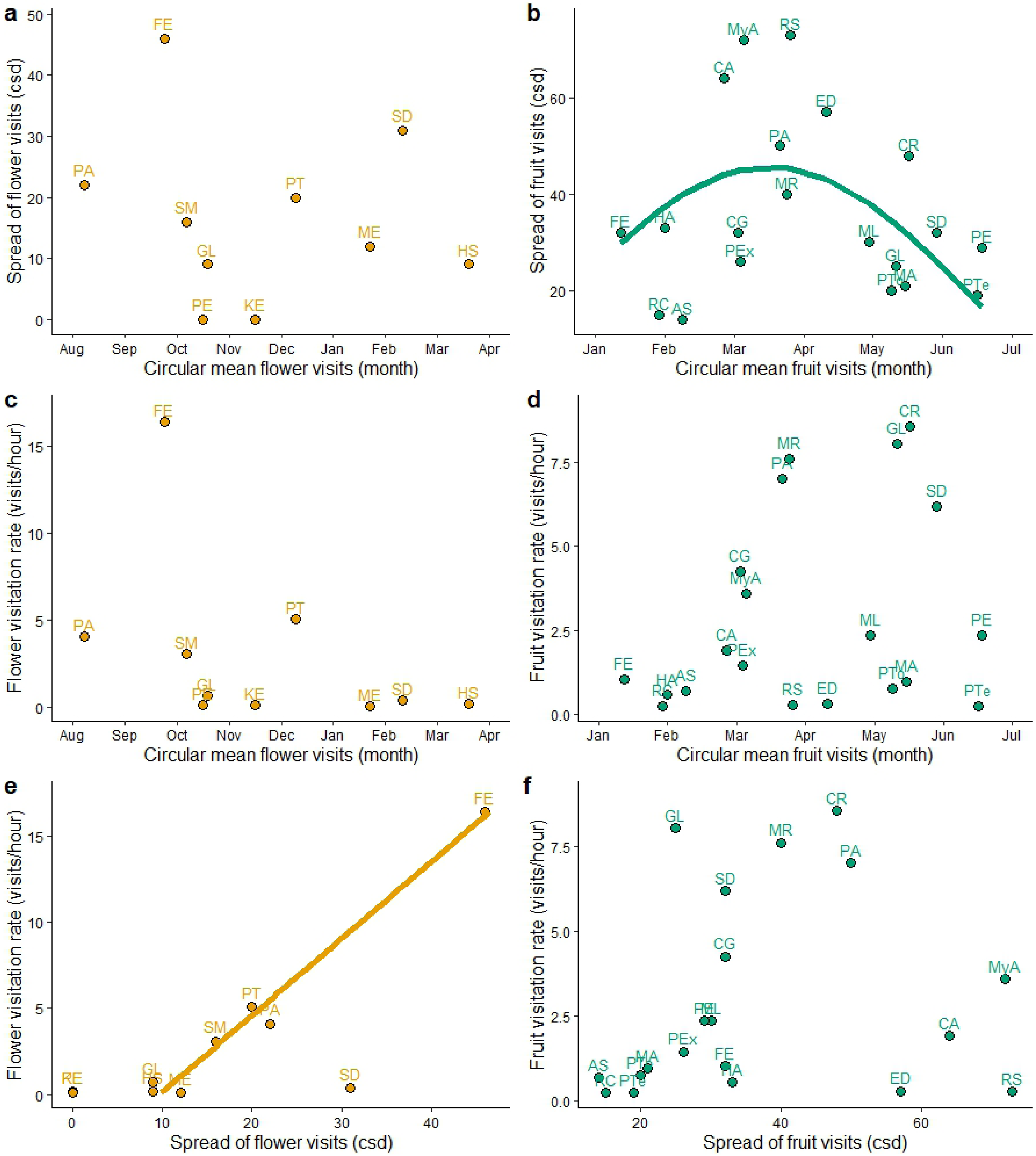

Figure 2. Pairwise relationships between (a) the circular mean (timing of peak visits) and circular standard deviation (temporal spread of visits, abbreviated as 'csd') of flower visits, (b) the circular mean and circular standard deviation of fruit visits, (c) the visitation rate and circular mean of flower visits, (d) the visitation rate and circular mean of fruit visits, (e) the visitation rate and circular standard deviation of flower visits, and (f) the visitation rate and circular standard deviation of fruit visits. Each point represents a plant species sampled from Zealandia ecosanctuary in Wellington, New Zealand, between 2006 and 2015. Visitation records were pooled across all sampling years and all bird species. Refer to Table 1 for plant species names corresponding to the codes in the plots. For a, b, c and d, the circular mean is represented using the corresponding months. Higher circular means indicate later dates of peaks in visits, and higher circular standard deviations indicate a broader temporal spread of visits. The solid green curve represents the sinusoidal relationship between the timing and temporal spread of fruit visits. The solid orange line represents the positive relationship between flower visitation rate and the temporal spread of flower visits. No line indicates that no relationship was detected.

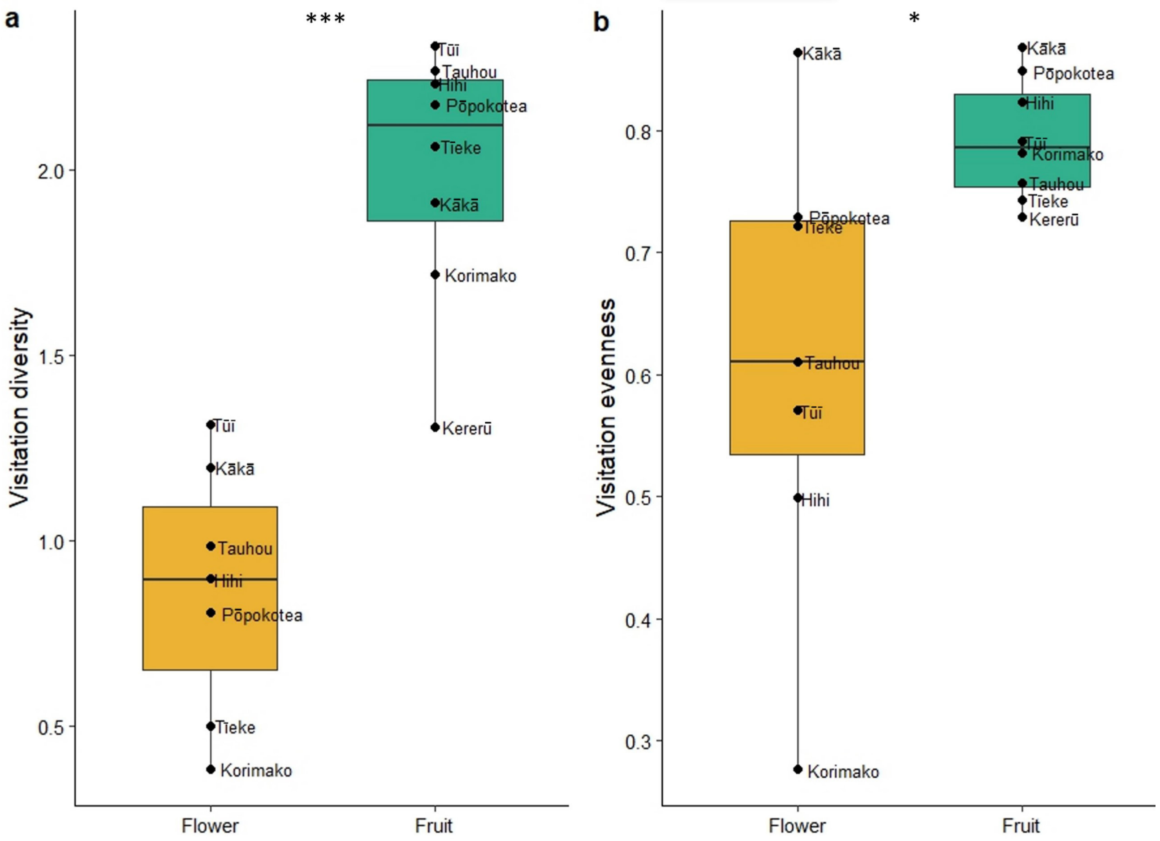

Figure 3. Boxplots representing the visitation diversity (Shannon diversity index) (a) and evenness (Pielou's evenness index) (b) of flower and fruit resources for each bird species sampled from Zealandia ecosanctuary in Wellington, New Zealand, between 2006 and 2015. Each point represents a bird species, with common names of birds indicated next to the corresponding points. Asterisks indicate significant differences between flower and fruit resources (*p < 0.05; ***p < 0.001). Visitation records were pooled across all sampling years and all plant species.

a few, high-reward species with short flowering phenophases (Stiles 1975; Rathcke & Lacey 1985), whereas the seasonal dynamics of fruit visitation seemingly followed the resource concentration hypothesis, with a mid-season abundance peak that promoted overlap and potentially facilitated more diffuse frugivore interactions (Herrera 1998; Jordano 2014).

The timing of peak visits to both flowers and fruits did not explain the visitation rates to individual plant species, indicating that factors other than seasonal timing may shape interaction frequency. Such factors may include avian abundance, morphological trait-matching, and phenological overlap (Sonne et al 2020; Peña et al. 2023). Visitation rates to flowers increased with a higher temporal spread of visits. This pattern was likely driven by *F. excorticata*, which exhibited both high visitation rates and an extended flowering period from June to January (Webb et al. 1988). When *F. excorticata* was excluded from the analysis, the relationship weakened, suggesting that birds follow the principles of optimal foraging theory, whereby highly abundant floral resources attract repeated and extended visitation windows, in contrast to more ephemeral resources that are exploited more briefly (Pyke et al. 1977).

Birds foraged broadly and evenly on fruits of different species, whereas floral interactions were more specialised, indicating greater competition among plant species for nectivores than frugivores (Kelly et al. 2010; Anderson et al. 2011). Tūī, hihi, and tauhou were highly generalised omnivores, exploiting a wide range of fruit resources, whereas kererū specialised on a limited subset of fruit species (Burns 2013b). The prolonged and overlapping availability of fruits, as evident in our findings, may represent a bet-hedging strategy, wherein plants mitigate the risk of reproductive failure by spreading the timing and conditions of fruit production (Schubert & Walters 2022). Such a strategy may confer an advantage to species with lower-quality fruits by increasing their likelihood of dispersal in a competitive environment (Snow 1965; Burns 2005; Palacio et al. 2021). In contrast, flowers showed shorter and more temporally distinct visitation windows, likely reflecting the need to concentrate flowering to maximise conspecific pollen transfer and align with peak pollinator activity (Rathcke & Lacey 1985; Elzinga et al. 2007).

Flower visitation was strongly skewed toward a single species, *F. excorticata*, which had the highest visitation rate of any species of flower or fruit. As one of five species visited for both its flowers and fruit (Burns 2013a), *F. excorticata* appears to be a particularly valuable resource for the avian community at Zealandia. *Fuchsia excorticata* trees are susceptible to large-scale defoliation and mortality caused by introduced mammals such as brushtail possums (*Trichosurus vulpecula*) (Pekelharing et al. 1998; Sweetapple & Nugent 1999), making them a vulnerable resource in areas where invasive pests are not actively managed. Broader surveys across forest types may uncover additional key plant species that serve as important food resources for birds at a local scale.

In addition to analysing seasonal patterns of bird-plant interactions, we present a multi-year dataset of field observations of bird-plant interactions in a regenerating forest in New Zealand. O'Donnell & Dilks (1994) previously published a similar dataset of bird-plant interactions collected over two years from a mixed podocarp-hardwood and beech forest in South Westland in the South Island of New Zealand. Comprehensive datasets such as those of O'Donnell & Dilks (1994) and the present study are important data sources for subsequent research on pollination and seed dispersal systems in New Zealand (e.g. Newstrom & Robertson 2005, Kelly et al. 2010, Burns 2012, Wotton & McAlpine 2015).

Long-term data highlight the ecological drivers and temporal dynamics that shape bird-plant mutualisms (e.g. Herrera 1998; Traveset et al. 2015; Anderson et al. 2021; Ohkawara et al. 2022). Multi-year studies also effectively capture infrequent yet important interactions in bird-plant networks (Weatherhead 1968; Herrera 1998). For instance, our data showed that kākā, hihi, and tūī visited the flowers of *Hoheria sexstylosa*, confirming the reports by Kelly et al. (2010) which listed *H. sexstylosa* as a "possible occasionally-visited entomophilous-flowered" plant. Previous studies have highlighted the cryptic importance of bird pollination in the New Zealand flora and the dearth of such descriptive data from sanctuaries (Castro & Robertson 1997; Anderson 2003; Kelly et al. 2010; Anderson et al. 2021). Birds could potentially pollinate all flowers they visit, even those that are not considered typically ornithophilous (Kelly et al. 2010). The ten flower species visited by birds in Zealandia comprised a mix of ornithophilous flowers (*F. excorticata*, *Knightia excelsa*, *M. excelsa*, *S. microphylla*, *P. tenax*), generalist flowers (*G. ligustrifolium*, *P. arboreus*), frequently-visited entomophilous flowers (*P. eugenioides*), and occasionally-visited entomophilous flowers (*S. digitata*) as listed by Kelly et al. (2010).

Introduced species often play complex roles in ecological networks (Traveset & Richardson 2014; Peralta et al. 2020). Correspondingly, there is mixed evidence for the role of introduced species in bird-plant mutualisms in New Zealand. For instance, introduced birds such as European blackbirds (*Turdus merula*) were previously considered to be relatively unimportant mutualists (Kelly et al. 2006). However, later studies suggest that in habitats where native frugivores became rare, blackbirds acted as important frugivores, interacting with a high diversity of plants (Burns 2012; García et al. 2014). Blackbirds were prominent frugivores in Zealandia throughout our study period, accounting for 750 fruit visits, making them the third most recorded frugivore after tauhou and tūī. Similarly, non-native plants are often incorporated into existing food webs, with neutral to negative effects on native animals (Schirmel et al. 2016; Nelson et al. 2017). Tree lucerne (*Chamaecytisus palmensis*) and Darwin's barberry (*Berberis darwinii*) were highly visited by native birds in Zealandia. For our study, we only considered native species to establish reference points for seasonal patterns in bird-plant interactions. However, the records of bird-plant interactions between non-native species are included in the online dataset (Appendix S1–S4).

Overall, our findings revealed complex temporal patterns in bird-plant interactions that addressed a key gap in our understanding of community-level mutualisms in New Zealand. Fruit visitation was more generalised and temporally widespread between species, whereas flower visitation was more specialised and temporally distinct, reflecting complementary patterns in bird-flower and bird-fruit interactions. With climate change shifting the timing of seasonal events (Tiusanen et al. 2020; Inouye 2022; Stephens et al. 2022) and human-driven disturbances like species introductions and habitat modifications threatening pollination and seed dispersal mutualisms (Neuschulz et al. 2016), long-term datasets like ours are crucial for assessing ecological and conservation outcomes in restored habitats. Future work should integrate detailed phenological data of flower and fruit production with avian visitation patterns to better understand seasonal resource preferences relative to availability.

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Supplementary material

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

Appendix S1. Monthly summaries of bird-plant interactions in Zealandia ecosanctuary in Wellington, New Zealand, between 2006 and 2015.

Appendix S2. Summaries of pairwise comparisons of circular distributions of bird-plant visitation for each species pair using Mardia-Watson-Wheeler's test for homogeneity of means with Bonferroni correction.

Appendix S3. Summary of results of pairwise relationships between circular means, circular standard deviations, and visitation rates for both flower and fruit resources.

Appendix S4. Sampling accumulation curves and estimates of sampling completeness for each calendar month.