Birds, fruit and nectar:

spatio-temporal patterns of regional bird abundance and

food availability in subtropical eastern Australia

A thesis submitted for the degree of Doctor of Philosophy

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The great escarpment; Dorrigo Plateau at right and upper Bellinger valley at left

Wompoo Fruit-doves (*Ptilinopus magnificus*)

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Abstract

Spatio-temporal patterns of animal abundance, and the factors explaining them, have seldom been studied at a regional scale. I sought to describe and explain patterns of bird abundance (for all birds, and for frugivores and nectarivores) by counting birds and measuring fruit and flower availability monthly for 24 months at 83 sites across a 300 000 ha region in subtropical eastern Australia. In particular, I wanted to examine the effects on abundance of climate, primary productivity, vegetation and food availability.

Patterns of fruit availability were similar in both years, but the spatio-temporal pattern of flowering differed between years because of irregular blossoming by eucalypts. Most variation in fruit and flowers was spatial; spatio-temporal variation was also important, but there was relatively little temporal variation. Vegetation type and primary productivity were the greatest influences on fruit availability; flowering was chiefly influenced by primary productivity and rainfall.

As with food availability, most variation in bird abundance was spatial: there were more birds in certain vegetation types and where mean food (fruit and flower) availability was higher. Spatio-temporal variation resulted from food tracking, whereby frugivores and nectarivores moved among localities and vegetation types in response to seasonal changes in the availability of fruit and flowers. However, spatio-temporal variation in consumer abundance was not as great as might have been expected, given the degree of spatio-temporal variation in food availability; this suggests that fruit and nectar were generally in over-supply during the study. Temporal variation in bird abundance was less marked than spatial or spatio-temporal variation, and was chiefly associated with variation in primary productivity, probably

because recruitment of juveniles and influxes of migratory insectivores occurred during times of high productivity; there was little net migration into or out of the study region by frugivores or nectarivores.

Of the explanatory factors I examined, food (fruit and flower) availability had the greatest influence on bird abundance. Because food availability differed among vegetation types, the association between vegetation and bird abundance was also strong. Although variables relating to primary productivity were important influences on food availability, they had only weak effects on bird abundance. The weakness of the productivity-abundance relationship was partly due to a combination of low spatial (but high temporal) variation in productivity and low temporal (but high spatial) variation in bird abundance. I would expect the relationship to be stronger in areas with greater spatial variation in productivity, or where long-distance migrants were a greater component of the avifauna.

My study represents an important advance in our understanding of the factors that influence animal abundance over large areas. Abundance is strongly influenced by food availability, which is in turn affected by climate, primary productivity and vegetation characteristics. Seasonal changes in food availability drive intra-regional bird movements among vegetation types and localities; such movements need to be considered in conservation planning, which is often premised on species having static distributions.

General declaration

In accordance with Monash University Doctorate Regulation 17.2 the following declarations are made:

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

This thesis includes five unpublished publications. The core theme of the thesis is that food availability, which is in turn influenced by primary productivity, vegetation and climate, is the main driver of spatio-temporal patterns of regional bird abundance. The ideas, development and writing of all the papers in the thesis were the principal responsibility of myself, the candidate, working within the School of Biological Sciences under the supervision of Dr Ralph Mac Nally.

The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research.

In the case of chapters 2-6, my contribution to the work involved the following:

Thesis chapter	Publication title	Publication status*	Nature and extent of candidate's contribution
2	A systematic approach to planting for the conservation of frugivorous birds	To be submitted	I conceived the study, performed all of the fieldwork and 80% of the statistical analyses, and was the primary author of the manuscript.
3	Patterns of regional nectar availability in subtropical eastern Australia: implications for plants and birds	To be submitted	I conceived the study, performed all of the fieldwork and 80% of the statistical analyses, and was the primary author of the manuscript.
4	How well do frugivorous birds track fruit availability at regional scales?	To be submitted	I conceived the study, performed all of the fieldwork and 50% of the statistical analyses, and was the primary author of the manuscript.
5	Regional scale resource tracking by nectarivorous birds	To be submitted	I conceived the study, performed all of the fieldwork and 50% of the statistical analyses, and was the primary author of the manuscript.
6	What drives the abundance of forest birds? Effects of food availability, primary productivity and vegetation	To be submitted	I conceived the study, performed all of the fieldwork and 50% of the statistical analyses, and was the primary author of the manuscript.

I have renumbered sections of papers in order to generate a consistent presentation within the thesis.

Signed: í

Date: í í í í í í í í í í í

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Massive thanks to Michael Collier for setting up the project database. Thanks to Dr Michael Forster from ICT for lending me the CI-130 Digital Plant Canopy Imager. Thanks to Terry Evans and Ian Montgomery for allowing me to use your terrific photos in presentations.

Thanks to the birds and forests of the Bellinger Valley; the two years I spent among you were an incredible gift.

The last and biggest thanks go to my wonderful wife, Sally. When I commenced this project, I had no idea how much it would be your burden too. Thankyou for your patience and understanding. And to Rosella, who began just as the bird surveys were ending, thanks for reminding me that there are more important things than PhDs.

Copyright Notices

Chapter 1   General Introduction

The concepts of distribution and abundance are intimately linked (Brown 1984), being
=aspects of the same problemø(Andrewartha and Birch 1954, p. 5). The distribution of
an organism is the result of spatial variation in its abundance; anything that affects
abundance will also affect distribution. Throughout this thesis, remarks on abundance
apply equally to distribution.

Food availability is a key driver of animal abundance, imposing an upper limit
on population size (White 2008). Other important influences on abundance include
climate and shelter (Andrewartha and Birch 1954). Climate may affect abundance
directly (e.g. through mortality of animals that exceed their physiological limits), or
indirectly, by influencing food availability (Andrewartha and Birch 1954). Shelter
affects abundance by providing safety from predators and by mediating the effects of
climate (Andrewartha and Birch 1954). Interactions with other animals, such as
predation and parasatism, may also affect abundance; however, consideration of such
higher-order processes is beyond the scope of this study.

Data on climatic variables such as temperature and rainfall are easily obtained,
but measuring the availability of food and shelter is more difficult. Because food and
shelter are influenced by vegetation, many studies of abundance have (explicitly or
implicitly) used vegetation characteristics as surrogates for food and shelter
availability (e.g. Ferrier et al. 2002).

A conceptual model of the interactive effects on abundance of food, climate
and vegetation is shown in Fig. 1.1. In this model climate, the key distal driver of
abundance, influences food availability in two ways: through its long-term effects on
vegetation, and through its short-term effects on plant growth (primary productivity),
which sets an upper limit on the amount of food that an ecosystem can provide.

Vegetation also influences productivity (which is higher in some vegetation communities than others: Melillo et al. 1993), as well as determining the allocation of productivity to different food types. For example, some vegetation communities (e.g. subtropical Australian rainforests) are rich in fruit and poor in nectar, while other communities (e.g. Australian heathlands) show the reverse pattern. The effects on abundance of food, climate/productivity and vegetation have often been examined in isolation, but few studies have sought to investigate them concurrently; thus, the validity of the model in Fig. 1.1, and the strength of the posited relationships, is unknown.

Climate, vegetation and food availability vary spatially, temporally, and spatio-temporally (i.e. where the spatial pattern changes over time). Variation in climate includes short-term seasonal patterns, inter-annual variations (e.g. El Nino Southern Oscillation cycles: Ropelewski and Halpert 1987) and long-term climate change (Hameed et al. 1980). Vegetation characteristics may vary seasonally (particularly in temperate regions where in winter many plants lose their leaves, or persist only as seeds) or over multi-year time-scales (e.g. as a result of succession: Purdie and Slatyer 1976). In some areas, food availability undergoes regular seasonal variations (Westcott et al. 2005); in others, particularly where rainfall is unpredictable, variation is irregular (Fredriksson 2006). Food availability may also undergo marked inter-annual variations (Fredriksson 2006).

Variations in food, shelter and climate might be expected to result in variations in animal abundance. Numerous studies have reported spatial, temporal, or spatio-temporal variation in the abundance of taxa including mammals (Laurance 1994), frogs (Toft 1980) and birds (Rey 1995). Factors found to explain variation in abundance include food availability (Cotton 2007); the availability of shelter (e.g. tree

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hollows: Smith and Lindenmayer 1988); vegetation characteristics such as density (Mills et al. 1991), floristics (Rotenberry 1985) and structural complexity (Macarthur and Macarthur 1961); primary productivity (Monkkonen et al. 2006); and climatic variables such as temperature and rainfall (Hawkins et al. 2003). Most studies of the relationship between food availability and abundance have been at small spatial scales (< 20 km^2). Partly because of the difficulty of measuring food, studies at larger scales have usually explained abundance in terms of climate, primary productivity and/or mapped vegetation types (e.g. Ferrier et al. 2002, Pautasso and Gaston 2005). There have been few attempts to compare the effects of food, vegetation, climate and productivity on organism abundance.

Birds are excellent subjects for studying spatio-temporal variation in abundance: they are conspicuous (and therefore relatively easy to count), and many species are sufficiently mobile to ÷sampleø large areas. Over half of the worldøs bird species make migratory movements of some kind (Berthold 2001), ranging from inter-continental migrations to relatively small-scale movements within a region. Intra-regional movements by birds have been noted in many parts of the world (Levey and Stiles 1992, Kimura et al. 2001, Thiollay 2002); examples include altitudinal migration (Burgess and Mlingwa 2000, Inouye et al. 2000) and shifts between vegetation types (Mac Nally 1995). Intra-regional movements may be of considerable ecological importance: in some places, transient (i.e. locally mobile) birds comprise the bulk of the avifauna (Poulin et al. 1993). Despite their prevalence, intra-regional movements are often ignored in the species distribution maps (Guisan and Zimmermann 2000) that underlie much conservation planning (e.g. Ferrier et al. 2002, Williams 2006), meaning that reserves may fail to protect the full extent of the habitat that a species or population relies on. Many intra-regional movements appear to be

driven by food tracking, the process whereby consumers follow the shifting distributions of foods such as insects (Lefebvre et al. 1994), nectar (Franklin and Noske 1999) and fruit (Telleria and Perez-Tris 2003).

Nectar and fruit are key foods for many birds, and birds perform vital roles as pollinators and seed dispersers of nectar- and fruit-producing plants. Plant-frugivore and plant-nectarivore mutualisms are important features in many ecosystems, particularly in the tropics and subtropics. In tropical forests, where around half of the bird biomass is supported by fruit (Fleming et al. 1987), up to 90% of tree and shrub species depend on vertebrate frugivores to disperse their seeds (Fleming et al. 1987). There are over 8,000 bird-pollinated species in the Americas alone (Nicolson and Fleming 2003), and nectarivory has driven the radiation of three major avian families: the new world hummingbirds (Trochilidae), the sunbirds (Nectariniidae) of Africa and Asia, and the Australasian honeyeaters (Meliphagidae). Unlike many other foods eaten by birds (e.g. insects), fruit is relatively conspicuous and easy to measure, making it feasible to document fruit availability at relatively large scales. Measuring nectar is more difficult, and studies of nectar availability have been limited to small areas (usually $< 20 \text{ km}^2$); at larger scales, flower abundance has sometimes been used as a proxy for nectar availability (e.g. MacNally and McGoldrick 1997).

The availabilities of fruit and nectar fluctuate annually (although not necessarily synchronously) in many parts of the world, resulting in regular ‑lean seasonsø when food for frugivores or nectarivores is scarce (Stiles 1980, Innis 1989); plants that provide reliable lean season fruit or nectar are likely to be of particular importance to birds (Peres 2000). Fruit and nectar availabilities also exhibit substantial spatio-temporal variation; compared to other food types, such as insects, the occurrence of fruit and nectar is extremely patchy and ephemeral (Fleming 1992).

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Birds may respond to such variation by tracking the changing distribution of food across the landscape, or by diet switching (i.e. consuming other food types during periods of fruit or nectar shortage). Species differ in their use of these strategies. At one extreme are fruit and blossom ‑nomads‑ highly mobile specialists that track fruit or nectar over great distances, sometimes > 1 000 km (Eby 1991, Holbrook et al. 2002). Conversely, diet switching allows the persistence of more-or-less sedentary generalists that eat fruit or nectar when available but subsist on other food types for long periods. Many species appear to combine both strategies, diet switching to an extent and tracking fruit or nectar over relatively short distances.

Many studies (e.g. Levey 1988, Blendinger et al. 2012) have shown that frugivore or nectarivore abundance in small areas (< 20 km^2) varies in response to fluctuations in food availability (i.e. that birds track the temporal availability of fruit and nectar at small spatial scales). However, studies over small areas can only speculate about where the ‑additional‑ birds may have come from or gone to. A more complete understanding of food tracking requires studies over large areas and (because patterns are dependent on the scale of analysis: Burns 2004) at multiple scales. Also, given that patterns of food availability may vary between years (Fredriksson 2006), studies should span at least two years. Most multi-year, multi-scale studies of food tracking at regional or greater scales have examined fruit-frugivore systems in temperate Europe (e.g. Guitian and Munilla 2008, Telleria et al. 2008). None of these studies has investigated the influence on abundance of factors other than food (e.g. climate, productivity or vegetation characteristics), or sought to provide a comprehensive account of food tracking by sampling the full range of vegetation types and climatic conditions in the region of interest.

In this thesis, I document spatio-temporal patterns of food (fruit and flower) availability and bird abundance in a 314 000 ha region centred on the Bellinger Valley in subtropical eastern Australia. The study region has a warm subtropical climate, with high annual rainfall (~1 700 mm) and a regular dry season between July and October. The dominant vegetation type is sclerophyllous forest with a canopy of ÷eucalyptsø (i.e. members of the closely related genera *Eucalyptus*, *Corymbia* and *Angophora*). The region contains areas of world-heritage listed rainforest (e.g. Dorrigo and New England National Parks) notable for their floristic diversity and a large number of threatened and/or geographically restricted species. The diverse avifauna includes many frugivores (24 spp. were recorded on-site during the study) and nectarivores (20 spp. were recorded), including several threatened species (e.g. the frugivorous wompoo fruit-dove *Ptilinopus magnificus* and nectarivorous swift parrot *Lathamus discolor*). I counted birds, fruits and flowers regularly (monthly for the most part) at 83 sites for 24 months, and used the data to model relationships between climate/primary productivity, birds and plants. I asked: (1) what are the spatio-temporal patterns of fruit and nectar availability?; (2) can these patterns be explained by vegetation and climate/primary productivity?; (3) which plant species or vegetation types are important sources of fruit or nectar?; (4) what are the spatio-temporal patterns of bird abundance (of frugivores, of nectarivores, and of all birds)?; (5) do frugivores and nectarivores track food?; and (6) what are the effects on bird abundance of climate/primary productivity, vegetation and food availability?

In Chapter 2 I document temporal patterns of fruit availability, identify important variables influencing variation in fruit availability, and develop a conceptual framework for prioritizing species to plant for the conservation of frugivorous birds. In Chapter 3 I describe and explain patterns of nectar availability,

and discuss their implications for nectarivore survival strategies and the evolution of flowering phenologies. The relationships between spatio-temporal patterns of frugivore biomass and fruit availability, and between nectarivore biomass and nectar availability, are explored in Chapters 4 and 5, respectively. In Chapter 6 I examine the relative effects of vegetation, productivity/climate and food (fruit and nectar) on the abundance of all birds and of three important feeding guilds (frugivores, nectarivores and insectivores). A general discussion of my findings is presented in Chapter 7.

Figure 1.1. A conceptual model of animal abundance. Food availability sets an upper limit on abundance. Climate/productivity (which are closely linked, because productivity varies in response to spatio-temporal variations in climate) influence abundance through their effects on food availability; climate may also influence abundance directly (e.g. through mortality of individuals that exceed their physiological limits). Vegetation influences abundance indirectly, through its effects on food, shelter and primary productivity (which differs between vegetation types). For the sake of clarity, some factors that may be important influences on animal abundance, but which are beyond the scope of this study (e.g. biotic interactions) have been omitted.

Declaration for Thesis Chapter 2

In the case of Chapter 2, the nature and extent of my contribution to the work was as follows:

Nature of contribution	Extent of contribution (%)
I conceived the study, performed all of the fieldwork and 70% of the statistical analyses, and was the primary author of the manuscript.	90%

The following co-authors contributed to the work:

Name	Nature of contribution
Dr Ralph Mac Nally	Ralph Mac Nally contributed ideas to the work and co-authored the manuscript.
Dr James Thomson	James Thomson assisted with statistical analyses and helped write the ‑modelling fruit availabilityø section.

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidateøs and co-authorsø contributions to this work.

Candidateøs Signature		Date
Main Supervisorøs Signature		Date

Chapter 2   A systematic approach to planting for the conservation of frugivorous birds

Abstract

Replanting is an important tool to reverse biodiversity declines caused by land clearing, but there have been few systematic attempts to determine which plant species should be used in revegetation. We identified priority species to plant for frugivore conservation by documenting seasonal cycles of fruit availability and avian frugivory for 24 months across a 300 000 ha region in subtropical eastern Australia. Fruit availability followed a consistent annual cycle, with a peak from February to April (austral summer and autumn) and a ‑lean seasonø from July to November (winter-spring). The most prolific source of fruit during the lean season was the camphor laurel *Cinnamomum camphora*, an invasive weed that is the subject of control programs. We suggest that the best species to plant are those that: provide food reliably every year; provide food during periods of scarcity; are native; are easy to cultivate; and are preferred by threatened and/or ecologically important consumers. Our study provides a conceptual framework for prioritizing species to use in revegetation, and stresses the importance of replacing exotic plants with natives that are equally reliable sources of food for the same suite of consumers and at the same times of year.

Introduction

Land clearing is a major threat to biodiversity in general (Brooks et al. 2002) and to frugivores in particular; in the tropical areas where deforestation rates are currently highest, frugivores frequently comprise the bulk of vertebrate biomass (Fleming et al. 1987). Frugivores threatened by land clearing include ‑charismaticø taxa such as toucans, hornbills and large primates (IUCN 2013). Reversing the impacts of deforestation on these and other species will require the revegetation of cleared land through a combination of ‑naturalø regeneration and replantings (Hobbs 1993, Kanowski et al. 2008).

Frugivores are crucial to ecosystem functioning: in tropical forests up to 90% of tree and shrub species rely on vertebrate frugivores such as birds, bats and primates for seed dispersal (Howe and Smallwood 1982). By spreading seeds from forest into cleared or regenerating areas, frugivores play an important role in facilitating revegetation (Neilan et al. 2006). Conversely, revegetation programs may benefit frugivores by increasing food availability.

The food available to frugivores varies seasonally. In most regions there are regular lean seasons when frugivore populations are limited by the scarcity of fruit (Fleming et al. 1987). Although the seasonal cycle of fruit availability may be predictable at the community level, the fruiting patterns of individual species are highly variable: many tropical and subtropical species have supra-annual or irregular fruiting patterns, and species that fruit every year are the exception (Fleming et al. 1987). Fruit quality (the proportion of fat and/or protein relative to water and carbohydrate: Fleming et al. 1987) also differs widely. Interspecific differences in fruiting patterns and fruit quality suggest that some plants may be more valuable to

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frugivores than others, but there have been few systematic attempts to identify which species might be best to include in revegetation programs.

We identified priority species to plant for frugivore conservation by documenting the seasonal cycle of fruit availability and frugivory over 24 months across a 314 000 ha region in subtropical eastern Australia. We reasoned that the best plants to use in revegetation are those that fruit every year, fruit during periods of scarcity, and are preferred by frugivores. The frugivore community in the study region consists mostly of birds and includes several threatened species (e.g. wompoo fruit-dove *Ptilinopus magnificus*, rose-crowned fruit-dove *P. regina*, superb fruit-dove *P. suberba* and barred cuckoo-shrike *Coracina lineata*: NSW Threatened Species Conservation Act 1995) whose numbers have been reduced by land clearing. Revegetation in subtropical eastern Australia is complicated by the importance of the exotic camphor laurel *Cinnamomum camphora* as a food for native frugivores (Neilan et al. 2006, Kanowski et al. 2008). Camphor laurel was introduced to Australia from Asia in the nineteenth century, and has become an invasive weed of pastures and native forests; it has a tendency to form monospecific stands, resulting in reduced diversity of plants and other organisms, and efforts are being devoted to its control (Scanlon and the Camphor Laurel Taskforce 2000). However, camphor laurel fruits are an important food source for many native frugivores, including threatened species such as the rose-crowned fruit-dove (Date et al. 1991); consequently, camphor laurel removal could lead to declines in frugivore populations unless offset by plantings of =equivalentø native species (Date et al. 1991, Date et al. 1996). A second aim of our study was to identify species to plant as replacements for camphor laurels.

Methods

Study region

The 314 400 ha study region is centred on the Bellinger Valley on the mid north coast of New South Wales, Australia, at $152^o 43øE$, $30^o 28øS$ (Fig. 2.1). Elevations range from sea level in the east to c. 1 600 m above sea level. There is a moist subtropical climate with hot, humid summers and warm, drier winters. Temperature maxima in the Bellinger Valley range from $30^o C$ (January) to $20^o C$ (July); minima range from $18^o C$ (January) to $5^o C$ (July). Rainfall (1 704 mm annually at Coffs Harbour) is highest in summer and autumn (mean March rainfall is 234 mm) and lowest in winter and spring (mean September rainfall is 61 mm).

Vegetation

Native vegetation persists over the majority of the study region (Fig. 2.1), mostly as large connected blocks rather than as isolates. About 25% of the original vegetation has been cleared since European settlement in the mid 1800s. The principal vegetation type is sclerophyll forest dominated by *Eucalyptus* spp. ; these produce woody fruits that are not eaten by frugivores. Wet sclerophyll forests (in which the understorey is dominated by fleshy-fruited plants) occupy 33% of the study region, and dry sclerophyll forests (in which fleshy-fruited plants are absent or uncommon) 23%. Subtropical rainforest (12%) has a more complex structure and a greater diversity of trees than temperate rainforest (7% of the study region), which has fewer vines, lianas and epiphytes, few or no large figs, and lower tree diversity. Weedy regrowth (1% of the study region) occurs where rainforest has been cleared and the land has later been abandoned; it often includes high densities of exotic species such as camphor laurel.

Site selection

We used ArcGIS 9.3 (ESRI) software and a survey gap analysis procedure (Ferrier et al. 2007) to select 54 sites that sampled the range of native vegetation types and environmental conditions; sites were circular plots of 30-m radius. We positioned another 18 sites in representative areas of rainforest (the GIS mapping used in site selection did not discriminate between rainforest types) and 11 sites in weedy regrowth, which at that stage had not been mapped. Apart from the weedy regrowth sites, all sites were located in pairs c. 400 m apart; the walk between paired sites allowed the collection of additional data on fruiting phenology (results not reported).

Field program

BAH visited each site regularly (usually monthly, sometimes more than once per month) from December 2007 to the end of November 2009, making 1 654 site visits that sampled 1 500 out of a possible 1 992 site-month combinations (24 months × 83 sites). Groups of nearby sites were visited on the same day, but to reduce possible systematic biases we randomized the order in which sites were visited in each group, and the order in which groups were visited in each month. During each 20-min site visit, BAH conducted a 7-min bird survey (results reported in Chapters 4 and 5), then spent 13 min counting fruit (and flowers: results reported in Chapter 3).

Measuring fruit

For each species in fruit during a site visit, BAH counted the number of plants fruiting and estimated the average number of full-sized fruits per plant. Only fruits known to be eaten by birds were included in calculations of fruit biomass. For species whose full-sized fruits change colour as they ripen (e.g. camphor laurel, giant pepper vine *Piper novaehollandiae* and brown beech *Pennantia cunninghamii*), we classed fruit as either ripe or unripe. Fruit biomass for each fruiting species was calculated by

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multiplying the number of plants in fruit by the average number of fruits per plant by the average wet fruit mass; the latter data were obtained by weighing × 20 fruits of each species in the field using a handheld spring balance. Fruit biomass was summed for all fruiting species to give the total fruit biomass for each site visit. Unripe camphor laurel fruits, which were not recorded in the diets of the focal bird species during the study, were excluded from measurements of fruit biomass. Where a site was visited more than once in a month, we used the average fruit biomass for that site-month in analyses.

Selection of focal birds

We chose to target our planting schema at rare, threatened and/or ecologically important birds, reasoning that increasing the food supply for these species would be of greater benefit than increasing the food supply for common birds. We selected species with relatively well-known diets to minimise any bias that might arise in our ranking system through incomplete dietary knowledge. Our focal birds were wompoo fruit-dove, rose-crowned fruit-dove (the only threatened frugivorous birds whose diets in subtropical eastern Australia are relatively well known), and the topknot pigeon *Lopholaimus antarcticus*, an important long-distance seed disperser.

Observations of frugivory

Each bird observed eating fruit on-site during a survey was counted as one observation. The mass of focal birds observed eating fruit on-site was summed for all surveys, using bird masses from Higgins and Davies (1996). We then divided the total mass of focal birds eating fruit on-site by the total number of fruiting plants on-site (summed for all surveys, so that a single plant recorded fruiting in three separate surveys would count as three fruiting plants). The resulting value was regarded as an

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index of fruit attractiveness (expressed as g of feeding bird per fruiting plant) for each plant species. We also recorded opportunistic observations of birds eating fruit off-site.

Environmental variables

Monthly data on rainfall at a 0.05^o grid scale for January 2007 to November 2009 were obtained from the Australian Water Availability Project (http://www.eoc.csiro.au/awap/, accessed 10/11/2010), and were used to derive rainfall totals for periods of periods of 2, 3, 6, 9 and 12 months prior to a given month. Data for mean monthly and annual evapotranspiration rates (0.1^o grid scale) and mean monthly and annual numbers of potential frost days (0.05^o grid scale) were obtained from the Australian Bureau of Meteorology (accessed 15/10/2010). GIS layers (100-m grid scales) for wetness index, moisture index, annual temperature (mean and minimum), mean annual solar radiation, mean annual rainfall and elevation were obtained from the New South Wales Department of Environment and Conservation. We used ArcGIS 9.3 (ESRI) to derive 100-m grid scale layers for ±distance from nearest watercourseø Data for Gross Primary Productivity (GPP) at 0.0025^o grid scale were obtained from the Australian National University (Berry et al. 2007) on 15/06/2011 and used to derive GPP totals for periods of periods of 6 and 12 months prior to a given month.

Modelling fruit availability

Because the sites we surveyed comprise only a small fraction of the study region, and may disproportionately represent some combinations of biophysical characteristics in relation to their occurrence (for instance, weedy regrowth and subtropical rainforest were over-sampled relative to their extents), we considered that a fruit availability

model would provide a more accurate representation of the temporal pattern of regional fruit availability than raw measurements. We used Boosted Regression Trees (Elith et al. 2008) to model fruit biomass for each site-month as a function of vegetation type, calendar month and the environmental variables listed above, then mapped the predicted fruit biomass for each of the 24 months of the study across the entire study region, at a resolution of 0.0025^{o}. We built the model using the gbm() package in R (R Core Team 2012) with default learning rate (0.001) and bag.fraction (0.5), maximum interaction depth (5), and 10-fold cross-validation to determine the optimum number of trees. We performed additional 10-fold cross validation on the full model-building procedure (including determination of optimum number of trees) to assess model performance. To calculate total monthly fruit availability across the study region, we summed the values of fruit availability for all grid cells for each month, excluding cells where vegetation type was mapped as cleared (where fruit availability was effectively zero) or urban (for which we lacked fruit availability data).

Ranking species for planting

We used a combination of field observations from this study and published literature (Frith 1952, 1957, Crome 1975, Frith 1982, Holmes 1987, Innis 1989, Higgins and Davies 1996, Church 1997, Floyd 2008) to derive a list of plant species known or likely to be eaten by the three focal birds. We scored each plant species according to four criteria: (1) the species øfruiting regularity; (2) the number of lean season (July to November) months in which the species is known to bear fruit; (3) the attractiveness of the species øfruit to birds; and (4) whether the species has been recorded in the diets of each of the three focal birds. With regards to fruiting regularity, we considered that species that provide fruit in all or most years are of greater conservation benefit to

frugivores than species that seldom provide fruit. Therefore, we assigned a score of 6 to species that fruit in all or most years; 4 to species that fruit in about 50% of years; and 2 to species that seldom fruit. These scores apply to species, rather than to individual plants. Thus, a score of 6 for a species does not mean that a given individual of that species will fruit every year, but that, in any given year, some individuals of that species will fruit. Data on fruiting regularity were derived from Floyd (2008), Innis (1989), Holmes (1987), Crome (1975) and the present study. We gave a species a score of 1 for each lean-season month in which it had been recorded fruiting, for a maximum total of 5, using fruiting data from the same sources. We scored the attractiveness to birds of an average fruiting individual of each plant species on a scale of 1-3, deriving our scores from data in Church (1997), Frith (1952, 1957, 1982), Innis (1989), Crome (1975) and the present study. We gave a plant species a score of 1 for each of the three focal bird species that had been recorded eating fruits from that species. Last, we assessed the suitability of each of the plant species for cultivation in discussions with local plant growers (C. Broadfoot and J. Ross, January 2013), scoring them on a scale of 1-3 according to how easy they were to propagate and grow.

Replacements for camphor laurel

To identify the best replacements for camphor laurel, we scored species as described above, except that instead of scoring 1 for each lean-season month in which a species had been recorded fruiting, we scored 1 for each month in the camphor laurel season (April to August) in which a species had been recorded fruiting.

Results

We recorded 102 species of fruiting plants with fruits known or likely to be eaten by birds. The species that contributed the most fruit were camphor laurel (26.7% of total fruit biomass), large-leaved privet *Ligustrum sinense* (10.8%), wild tobacco *Solanum mauritianum* (7.0%), white cedar *Melia azedarach* (6.8%), giant pepper vine (6.1%) and jackwood *Cryptocarya glaucescens* (4.2%).

Seasonal cycle of fruit availability

The seasonal cycle of fruit availability was similar in the two years of the study, with a peak from February to April and a lean season from July to November (Fig. 2.2). The Boosted Regression Tree model explained fruit availability reasonably well: the naïve model rank correlation was 0.52, and the mean cross-validation rank correlation 0.37. Vegetation type and gross primary productivity (12-monthly, 6-monthly and monthly) were the most important influences on fruit biomass, explaining 17%, 15%, 9% and 8% of variation, respectively (Table 2.1).

Lean season fruiting species

The species that produced the most lean season fruit were camphor laurel, wild tobacco, brown beech *Pennantia cunninghamii*, giant pepper vine (unripe) and several figs *Ficus* spp. (Fig. 2.3). The species that produced the most lean-season fruit for the focal birds were camphor laurel, brown beech, figs, and the beach and common acronychias (*Acronychia imperforata* and *A. oblongifolia*, respectively).

Observations of frugivory

Camphor laurel, giant pepper vine, bangalow palm *Archontophoenix cunninghamiana*, giant strangler-fig *Ficus watkinsiana* and white cedar *Melia azedarach* were the species on which the focal birds were most often observed feeding (Table 2.2). In terms of grams of feeding bird per fruiting plant (our index of

attractiveness to birds), the highest scoring species were blue quandong *Elaeocarpus grandis* and white beech *Gmelina leichhardtii*, followed by small-leaved fig *Ficus obliqua*, giant pepper vine, white cedar and camphor laurel (Table 2.2).

Priority species for planting

The highest priority species for use in rainforest plantings are shown in Table 2.3; the full list of the 151 plant species known or likely to be eaten by the focal bird species, and their ranking for use in plantings, is presented in Supplementary Table S1. The only species to receive the highest possible priority score were large figs (*Ficus macrophylla, F. obliqua, F. rubiginosa, F. superba var. henneana and F. virens*). Other species that scored highly were *Acronychia* spp., native tamarind *Diploglottis australis*, saffronheart *Halfordia kendack*, native olive *Olea paniculata* and bangalow palm.

The best replacements for Camphor laurel are shown in Table 2.4 and Supplementary Table S1. The only species to receive the highest possible priority score were large figs (*Ficus macrophylla, F. obliqua, F. rubiginosa, F. superba var. henneana and F. virens*). Other native species that scored highly were saffronheart, silver basswood *Polyscias elegans*, pigeonberry ash *Cryptocarya erythroxylon* and common acronychia.

Discussion

A framework for prioritizing plant species for revegetation

Our study provides a conceptual framework for addressing a question faced by all revegetation projects: what to plant? We consider that the best species for planting are those that: provide food reliably every year; provide food during periods of scarcity; are native; are easy to cultivate; and are preferred by important consumers. We used

these criteria to prioritize species to plant for the conservation of three frugivorous bird species (Table 2.3) and as replacements for the camphor laurel, an invasive weed that has become a valuable food for native frugivores (Table 2.4). Although our study relates to frugivores in subtropical eastern Australia, the framework we present is applicable to a range of taxa, from a range of feeding guilds, in many parts of the world.

Selecting focal taxa (i.e. the taxa that the plantings will eventually benefit) allows revegetation programs to target species most in need of conservation. Focal taxa might include entire feeding guilds, or be limited to threatened and/or ecologically important species. The choice of species to plant is likely to have the greatest effect on primary consumers (e.g. folivores, frugivores, nectarivores and granivores), most of which eat a limited range of plant species; higher order consumers, by contrast, are likely to be less affected by the floristic composition of plantings. We targeted our plantings at frugivores, the most speciose guild of threatened primary consumers in our study region (NSW Threatened Species Conservation Act 1995). Rather than aiming to conserve all frugivores, we focused on three species: the two threatened frugivores whose diets are best known (wompoo and rose-crowned fruit-doves) and the topknot pigeon, an important long-distance seed disperser. Given the extensive overlap between the diets of the focal species and those of many other frugivores in the study region, revegetation projects using the highest-scoring plants in Table 2.3 are likely to also increase the food supply for non-focal species.

The core of our framework is the identification of plant species that provide reliable food during periods of scarcity; this requires data on the seasonality and reliability of food plants and the dietary preferences of consumers. By supplementing

field observations with published data, we produced a list of fruiting species known or likely to be eaten by the focal birds. We then used observations and published data to identify the fruiting season of, and degree of frugivore preference for, each plant species. The temporal scope of our study was insufficient to assess the reliability of many fruiting species; however, we were fortunate in being able to draw on two long-term studies of fruiting phenology from localities that shared many plant species with our study region (Innis 1989, Church 1997), as well as observations by an experienced rainforest botanist (A. Floyd, pers. comm., August 2012). Long-term data such as these are essential to assess fruiting reliability.

The availability of foods such as leaves (Wolda 1978), seeds (Renton 2001), nectar (Woinarski et al. 2000) and fruit (Westcott et al. 2005) varies predictably in most parts of the world, with regular ‑lean seasonsø when food is scarce. We found that fruit availability in the study region followed a consistent annual cycle: there was a lean season from July to November (the austral winter and spring) and a peak from February to April (summer and autumn). This accorded with previous studies of fruiting phenology and frugivory in subtropical eastern Australia (Holmes 1987, Innis 1989, Church 1997).

Assuming that consumer abundance is limited by food availability during periods of scarcity (Wiens 1977, 1989), then increasing the supply of lean-season fruit should increase frugivore population sizes. The greatest provider of lean-season fruit in our study region was the invasive camphor laurel (discussed below). The native species that produced the most lean-season fruit for the focal birds were brown beech, figs, and the beach and common acronychias. Over 20 plant species have been identified as sources of lean season fruit by previous studies in subtropical eastern Australia (Frith 1957, Holmes 1987, Innis 1989, Date et al. 1991, Church 1997);

however, apart from general agreement on the importance of camphor laurel and figs, there is little consensus between studies: the picture that emerges is one of considerable local and inter-annual variation.

The key outcome of our framework is the ranking of plant species for use in revegetation (Table 2.3). The scoring system we employed, and the weightings we assigned to each criterion, were necessarily somewhat arbitrary, but we consider that our criteria represent the critical factors that determine the value of plant species to consumers. Recent attempts to identify ‑keystoneø fruiting species (i.e. those of particular importance in maintaining frugivore populations) have used the same criteria as we did, plus the criterion of ubiquity/abundance, which is not relevant in selecting species to plant (Peres 2000, Westcott et al. 2005). We assigned roughly equal weights to our three main criteria, awarding a maximum score of 5 for fruiting seasonality (to species that have been recorded fruiting in every month of the lean season), 6 for fruiting reliability (to species that fruit every year), and 6 for frugivore preference (to fruits that are sought after by birds and have been recorded in the diets of the three focal frugivores). We did not score plants for ‑nativenessø, but we have indicated exotics and included range descriptions for Australian species in Table 2.3, on the assumption that land managers would not wish to plant species outside their natural ranges. The ‑suitability for cultivationø scores, while not included in our final rankings, are provided as a guide to which species are likely to be stocked by commercial nurseries, and which species will best repay efforts at propagation and growth.

Priority species for plantings

Large figs, beach and common acronychias, native tamarind, saffronheart, and bangalow palm scored highest under our ranking system (Table 2.3). The large figs

scored well partly because their asynchronous fruiting patterns mean that fruit is available on at least one plant of each species throughout the year, including in every month of the lean season. However, the fruiting patterns of the figs in the study region differ between individuals, and there is a reasonable likelihood that a given plant will not fruit during the lean season, or at any rate not every year. To ensure a supply of lean season fruit, therefore, it would be necessary to plant a large number of figs, from as many local parent trees as possible. The other highly ranked species in Table 2.3 are synchronous fruiters, i.e. they have a distinct fruiting season with all individuals producing fruit at roughly the same time. Planting an acronychia, a native tamarind or a saffronheart should therefore increase the supply of lean-season fruit. The bangalow palm differs from the other highly ranked species in that its usual fruiting season is from January to March. However, individuals in open positions, such as most gardens and revegetation projects, often bear fruit as early as September, meaning that bangalow palms planted in open positions are likely to increase the supply of lean season fruit for the focal birds.

A good revegetation program would involve planting a range of the higher priority plants in Table 2.3. There are two reasons for this: first, the greater the diversity of fruiting species available, the greater the likelihood that, should one species fail, another species will provide compensatory fruit. Second, frugivore abundance increases with increasing fruit diversity, irrespective of total fruit biomass (Chapter 4, Tables 4.1 and 4.2).

We also recommend clumping plantings so as to provide, in season, a large quantity of fruit in a small area; some species (e.g. topknot pigeon) seem to prefer feeding where fruit is spatially concentrated, whether in the form of a single prolific

tree (e.g. a large fig or camphor laurel) or of a cluster of less prolific trees (e.g. common acronychias or bangalow palms).

The camphor laurel

The greatest provider of lean-season fruit in our study region was the exotic camphor laurel, which contributed more than four times as much fruit (by biomass) as the most prolific native species. We observed the three focal bird species (including a group of ten wompoo fruit-doves and flocks of up to 200 topknot pigeons) feeding in camphor laurels, and between about April and July of both years the distributions of rose-crowned fruit-doves and topknot pigeons appeared to be largely governed by the distribution of fruiting camphor laurels. An important attribute of the camphor laurel is its reliability: the species has fruited prolifically in every year for which we have records (2006-2013; unpublished data), and we are not aware of any reports of years in which camphor laurels failed to fruit.

Camphor laurels were introduced to Australia from Asia in the mid 19th century and were widely planted as shade trees (Scanlon and the Camphor Laurel Taskforce 2000). Frith (1957) recounts how, following the failure of their usual food sources in the autumn of 1955, topknot pigeons began feeding on camphor laurel fruits for the first time. The spread of camphor laurels may have been hastened by their use by topknot pigeons: anecdotal reports suggest that camphor laurels were not widely naturalized in the study region until the 1960s and 1970s. Today camphor laurels are abundant throughout subtropical eastern Australia, where they occur in pastures, in weedy regrowth, and as seedlings in the understorey of native forests. Their impacts include reducing the diversity of native plants, destabilizing stream banks, and poisoning fish (Scanlon and the Camphor Laurel Taskforce 2000). The

camphor laurel is classified as a noxious weed over much of its Australian range and is the subject of control programs (Scanlon and the Camphor Laurel Taskforce 2000).

The story of the camphor laurel is mirrored by those of other invasive species. Exotic plants have become important items in the diets of native fauna in many parts of the world, including Africa (Voigt et al. 2011), North America (Bartuszevige and Gorchov 2006, Gleditsch and Carlo 2011) and Asia (Corlett 2005). The incorporation of invasive plants into the diets of native species poses a dilemma for conservation managers, who find themselves confronted with the contradictory imperatives of conserving native animals while eradicating the exotic plants that feed them (Gleditsch and Carlo 2011).

One suggested solution to this dilemma is to replace invasive plants with equivalent native species (Williams and West 2000, Gosper et al. 2005). Gosper and Vivian-Smith (2006, 2009) trialled several approaches for identifying native equivalents to exotic fruiting plants, concluding that methods involving comparing fruit traits and/or known consumers produced the best results. We ranked native replacements for the camphor laurel using a modified version of our framework for prioritizing species for revegetation. We consider that the best replacement species for the camphor laurel are those that: fruit reliably every year; fruit in the same months as the camphor laurel; are native; are easy to cultivate; and are preferred by the focal species. The main difference between our approach and those trialled by Gosper and Vivian Smith (2006, 2009) is the inclusion of fruiting reliability in our selection criteria. We consider this to be an important addition, because the camphor laurel fruits every year, and replacement species that do not will provide no food for frugivores in some years.

Overview

We present a conceptual framework for prioritizing plant species for use in revegetation. The best species to plant are those that: provide food reliably every year; provide food during periods of scarcity; are native; are easy to cultivate; and are preferred by threatened and/or ecologically important consumers. Similar criteria can be applied to select native replacements for invasive weeds that have been incorporated into the diets of indigenous fauna. Native replacements for invasive species should include plants that are equally reliable sources of food for the same suite of consumers and at the same times of year.

Table 2.1. Relative influence on fruit biomass of variables in Boosted Regression

Tree model (only variables scoring over 4 are shown). Relative influences sum to 100.

Variable	Relative influence
Vegetation type	17.1
GPP of previous 12 mo	14.8
GPP of previous 6 mo	9.0
Monthly GPP	7.6
Rainfall of previous 12 mo	4.5
Elevation	4.5
Distance to nearest water-course	4.4
Mean annual solar radiation	4.0

Table 2.2. Observations of focal bird species eating fruit during study. OPP = opportunistic observation(s) of species eating fruit. * denotes exotic species.

Common name	Scientific name	Total number of fruiting plants on-site during surveys	Number of observations of birds eating fruit on-site				Grams of feeding bird per fruiting plant (focal species only)
			Rose-crowned fruit-dove	Topknot pigeon	Wompoo fruit-dove	Total	
Camphor laurel*	*Cinnamomum camphora** (ripe)	365	4	163	20	187	266
Giant pepper vine (ripe)	*Piper novaehollandiae* (ripe)	53	1	56	7	64	631
Bangalow palm	*Archontophoenix cunninghamiana*	126	OPP	44	4	48	202
Giant strangler-fig	*Ficus watkinsiana*	304	0	0	19	19	28
White cedar	*Melia azedarach*	24	0	0	17	17	322
Blue quandong	*Elaeocarpus grandis*	7	0	15	OPP	15	1153

Small-leaved fig	*Ficus obliqua*	11	0	10	5	15	696
Jackwood	*Cryptocarya glaucesens*	36	0	3	11	14	184
Moreton Bay fig	*Ficus macrophylla*	26	0	3	4	7	132
White beech	*Gmelina leichhardtii*	2	0	0	4	4	910
Crabapple	*Schizomeria ovata*	36	0	0	2	2	25
Brown beech (ripe)	*Pennantia cunninghamii* (ripe)	39	0	0	2	2	23
Myrtle ebony	*Diospyros pentamera*	21	2	0	0	2	10
Yaroong	*Cissus sterculiifolia*	145	0	0	2	2	6
Rose walnut	*Endiandra discolor*	1	0	OPP	0	0	0
Beach acronychia	*Acronychia imperforata*	116	OPP	OPP	0	0	0
Common	*Acronychia oblongifolia*	9	OPP	OPP	OPP	0	0

acronychia							
Red ash	*Alphitonia excelsa*	84	0	0	OPP	0	0
Rose myrtle	*Archirhodomyrtus beckleri*	58	OPP	OPP	0	0	0
Kangaroo vine	*Cissus antarctica*	140	0	OPP	0	0	0
Blueberry ash	*Elaeocarpus reticulatus*	279	0	OPP	0	0	0
Cheese tree	*Glochidion ferdinandi*	64	0	0	OPP	0	0
Large-leaved privet*	*Ligustrum lucidum**	80	0	0	OPP	0	0
Brown beech (unripe)	*Pennantia cunninghamii* (unripe)	11	0	0	OPP	0	0

Table 2.3. Ranking of species (excluding exotics) for planting to conserve focal birds. A fruiting regularity score of 6 indicates that the species fruits in all most years; 4 that the species fruits in approximately 50% of years; and 2 that the species fruits in less than 50% of years. * = the species seldom consumes this fruit in our study region. The ‑suitability for cultivationø values, while not included in total score, are provided as a guide to which species are likely to be stocked by commercial nurseries, and which species will best repay efforts at propagation and growth.

Common name	Scientific name	Growth Form	Fruiting regularity score (2, 4 or 6)	Number of lean season (July-November) months in which species fruits (0-5)	Attractiveness to birds of average fruiting plant (1-3, where 1 = birds seldom present in plant, and 3 = birds often present in plant,)	Eaten by wompoo fruit-dove?	Eaten by rose-crowned fruit-dove?	Eaten by topknot pigeon?	Suitability for cultivation (1-3, where 1 = difficult to grow and 3 = easy to grow)	Total score
Moreton Bay fig	*Ficus macrophylla*	Tree	6	5	3	1	1	1	3	17
Small-leaved fig	*Ficus obliqua*	Tree	6	5	3	1	1	1	3	17
Port Jackson fig	*Ficus rubiginosa*	Tree	6	5	3	1	1	1	3	17
Deciduous fig	*Ficus superba var. henneana*	Tree	6	5	3	1	1	1	3	17

White fig	*Ficus virens*	Tree	6	5	3	1	1	1	?	17
Giant strangler-fig	*Ficus watkinsiana*	Tree	6	5	3	1	1	1	2	17
Common acronychia	*Acronychia oblongifolia*	Tree	6	5	2	1	1	1	2	16
Native tamarind	*Diploglottis cunninghamii*	Tree	6	4	3	1	1	1	3	16
Beach acronychia	*Acronychia imperforata*	Tree	6	5	2	0	1	1	1	15
Bangalow palm	*Archontophoenix cunninghamiana*	Tree	6	3	3	1	1	1	3	15
Saffronheart	*Halfordia kendack*	Tree	6	5	2	1	0	1	2	15
Green bolly gum	*Neolitsea australiensis*	Tree	6	5	2	1	0	1	3	15
Glossy acronychia	*Acronychia laevis*	Tree	6	4	2	0	1	1	?	14
Ylang-ylang	*Cananga odorata*	Tree	6	5	2	1	0	0	?	14
Pigeonberry ash	*Cryptocarya erythroxylon*	Tree	4	4	3	1	1	1	?	14

Silky myrtle	*Decaspermum humile*	Tree	6	5	2	0	1	0	2	14
Blue quandong	*Elaeocarpus grandis*	Tree	4	4	3	1	1	1	1	14
Cheese tree	*Glochidion ferdinandi*	Tree	6	5	1	1	0	1	2	14
Giant pepper vine	*Piper novaehollandiae*	Vine	6	2	3	1	1	1	?	14
Featherwood	*Polyosma cunninghamii*	Shrub	6	5	1	1	1	0	2	14
Blush coondoo	*Pouteria queenslandica*	Tree	6	4	2	1	0	1	?	14
Red apple	*Syzygium ingens*	Tree	6	4	2	1	0	1	?	14

Table 2.4. Ranking of species (excluding exotics) as replacements for camphor laurels. * = the species seldom consumes this fruit in our study region.

Common name	Scientific name	Growth form	Fruiting regularity score (2, 4 or 6)	Number of camphor laurel months in which species fruits (0-5)	Attractiveness to birds (1-3)	Eaten by wompoo fruit-dove?	Eaten by rose-crowned fruit-dove?	Eaten by topknot pigeon?	Suitability for cultivation (1-3, where 1 = difficult to grow and 3 = easy to grow)	Total score
Moreton Bay fig	*Ficus macrophylla*	Tree	6	5	3	1	1	1	3	17
Small-leaved fig	*Ficus obliqua*	Tree	6	5	3	1	1	1	3	17
Port Jackson fig	*Ficus rubiginosa*	Tree	6	5	3	1	1	1	3	17
Deciduous fig	*Ficus superba var. henneana*	Tree	6	5	3	1	1	1	3	17

Common name	Scientific name	Form								
White fig	*Ficus virens*	Tree	6	5	3	1	1	1	?	17
Giant strangler-fig	*Ficus watkinsiana*	Tree	6	5	3	1	1*	1*	2	17
Common acronychia	*Acronychia oblongifolia*	Tree	6	5	2	1	1	1	2	15
Saffronheart	*Halfordia kendack*	Tree	6	5	2	1	0	1	2	15
Green bolly gum	*Neolitsea australiensis*	Tree	6	5	2	1	0	1	3	15
Pigeonberry ash	*Cryptocarya erythroxylon*	Tree	4	4	3	1	1	1	?	15
Kangaroo vine	*Cissus antarctica*	Vine	6	2	1	1	1	1	?	15
Silver basswood	*Polyscias elegans*	Tree	6	1	2	1	1	1	?	15
White cedar	*Melia azedarach*	Tree	6	0	3	1	0	1	1	15
Native tamarind	*Diploglottis cunninghamii*	Tree	6	4	3	1	1	1	2	14
Bangalow palm	*Archontophoenix cunninghamiana*	Tree	6	3	3	1	1	1	3	14

Glossy acronychia	*Acronychia laevis*	Tree	6	4	2	0	1	1	3	14
Cheese tree	*Glochidion ferdinandi*	Tree	6	5	1	1	0	1	?	14
Featherwood	*Polyosma cunninghamii*	Shrub	6	5	1	1	1	0	2	14
Red apple	*Syzygium ingens*	Tree	6	4	2	1	0	1	2	14
Alexandra palm	*Archontophoenix alexandrae*	Tree	6	3	3	0	0	1	?	14
Blueberry ash	*Elaeocarpus reticulatus*	Tree	6	4	1	1	0	1	3	14
Native olive	*Olea paniculata*	Tree	4	3	3	1	1	1	?	14
Water vine	*Cissus hypoglauca*	Vine	6	1	2	1	0	1	1	14
Crabapple	*Schizomeria ovata*	Tree	6	1	2	0	1	1	2	14

Figure 2.1. Study region, showing survey sites and extent of vegetation cover.

Figure 2.2. Monthly fruit availability. The dashed line shows modelled fruit biomass (in tonnes) for the entire study region, derived from the Boosted Regression Tree model. The solid line shows the sum of fruit biomass (in kg) measured on-site. Because the sites we surveyed comprise only a small fraction of the study region, and may disproportionately represent some combinations of biophysical characteristics in relation to their occurrence (for instance, weedy regrowth and subtropical rainforest were over-sampled relative to their extents), we consider that the modelled fruit biomass values are likely to be a more accurate representation of the temporal pattern of fruit availability in the region than the raw measurements.

Figure 2.3. Total on-site fruit biomass during the lean season (July to November), summed over the two years of the study. * = exotic species. ** = fruited in first year of study only. **** = species represented by only a single individual.

Declaration for Thesis Chapter 3

In the case of Chapter 3, the nature and extent of my contribution to the work was as follows:

Nature of contribution	Extent of contribution (%)
I conceived the study, performed all of the fieldwork and 70% of the statistical analyses, and was the primary author of the manuscript.	90%

The following co-authors contributed to the work:

Name	Nature of contribution
Dr Ralph Mac Nally	Ralph Mac Nally contributed ideas to the work and co-authored the manuscript.
Dr James Thomson	James Thomson assisted with statistical analyses and helped write the =modelling nectar availabilityø section.

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidateøs and co-authorsø contributions to this work.

Candidateøs Signature		Date
Main Supervisorøs Signature		Date

Chapter 3   Patterns of regional nectar availability in subtropical eastern Australia: implications for plants and birds

Abstract

Aim. To document and explain patterns of regional nectar availability for birds.

Location. A 300 000 ha region in subtropical eastern Australia.

Methods. We measured flowering at 83 sites in bushland (i.e. natural vegetation) and 8 sites in gardens monthly for 24 mo. To estimate nectar availability, we combined flower-counts with a nectar index derived from the rate at which birds fed on the flowers of different plant species. We modelled nectar availability as a function of environmental variables such as vegetation type, rainfall and primary productivity (derived from satellite telemetry).

Results. The most important influences on nectar availability were primary productivity (summed over 12 mo) and rainfall (summed over 6 mo). Nectar availability in bushland varied widely between mo, and at times was close to zero. Temporal and spatio-temporal patterns in bushland differed between the two years of the study, due mostly to irregular flowering by a few species of *Eucalyptus*; the sole consistent temporal pattern was a lean season in spring (August-September). Coastal vegetation was a reliable source of prolific nectar for much of the year, including during the lean season. Gardens produced prolific nectar throughout the year, with an August-October peak. Hemiparasitic mistletoes in bushland provided small amounts of nectar year-round.

Conclusions. 1. Periods of scarcity occurred when low rainfall limited the capacity of plants to produce nectar; at these times the main nectar producers were plants with 'privileged' access to water. 2. Obligate nectarivory in the study region is likely to be confined to birds that are small (and hence able to subsist on mistletoe nectar) and/or extremely mobile. Except in gardens, larger nectarivores with sedentary populations must survive on foods other than nectar for lengthy periods. 3. Garden plantings may benefit birds by providing nectar during times of scarcity.

Introduction

Mutualistic relationships between plants and animals have evolved because both parties benefit. In plant-nectarivore relationships, animals receive food (nectar), and plants are pollinated. Mutualisms between plants and nectarivorous birds are common in many terrestrial ecosystems: there are over 8,000 bird-pollinated species in the Americas alone (Nicolson and Fleming 2003), and nectarivory has driven the radiation of three major avian families: the new world hummingbirds (Trochilidae), the sunbirds (Nectariniidae) of Africa and Asia, and the Australasian honeyeaters (Meliphagidae).

Because most plant species flower for only part of the year, nectarivorous birds typically depend on multiple plant species for food. The persistence of diverse assemblages of avian nectarivores attests to the success of plant communities in providing nectar over evolutionary time-scales. A possible contributor to this success is staggered flowering, whereby different species flower at different times of year. Staggered flowering may result in a more or less continuous supply of nectar over time, thereby preventing the extinction of nectarivore populations. This is the case in, for example, the neotropics, where sequentially flowering species provide year-round food for hummingbirds (Stiles 1980, Cotton 2007). The development of staggered flowering is thought to have been driven by competition for pollinators (Levin and Anderson 1970, Waser 1978).

Even where flowering is staggered, climatic constraints mean that community-wide nectar availability typically undergoes temporal fluctuations, with regular or irregular ‑lean seasonsø when nectar is scarce (Smith-Ramirez and Armesto 1994, Brown and Hopkins 1996, Malizia 2001, Brady 2009). Irregular fluctuations are

particularly common in Australia, where eucalypts (the genera *Eucalyptus*, *Corymbia* and *Angophora* in the Myrtaceae) are important nectar-producing species. Although eucalypts may produce large quantities of nectar (Law and Chidel 2008), most species flower unreliably, at intervals of several years (Birtchnell and Gibson 2006).

Spatial and temporal variations in community-wide nectar production result in a continually changing nectar ‑mosaicø (Woinarski et al. 2000). Nectarivorous vertebrates respond to variations in nectar availability by diet switching and/or nectar tracking. Diet switching involves coping with nectar shortages by consuming other food types such as insects, manna, honeydew, lerps and fruit (Paton 1980); most nectarivores appear capable of diet-switching to some extent. Highly mobile species also have the option of tracking the changing distribution of nectar across the landscape: flying-foxes and parrots may travel distances of tens or hundreds of km in search of nectar (Cannon 1984, Eby 1991, Saunders and Heinsohn 2008).

There have been few attempts to document patterns of nectar availability at the large scales relevant to many wide-ranging nectarivores (and to the plants they pollinate). Woinarski et al. (2000) combined vegetation mapping with information on the flowering seasons and nectar output of plants to produce a set of monthly ‑nectar mapsø for northern Australia. Eby and Law (2008) used similar methods to create bi-monthly maps of grey-headed flying-fox *Pteropus poliocephalus* habitat in eastern Australia. Both Woinarski et al. (2000) and Eby and Law (2008) mapped nectar availability across a ‑typicalø year. Because of the irregular flowering patterns of some plants, particularly eucalypts (Law et al. 2000), the conditions actually encountered by nectarivores may differ substantially from those in a typical year.

We documented patterns of nectar availability over 24 months across a 314 000 ha region in subtropical NSW, eastern Australia. The study region is home to

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many nectarivorous birds, including several threatened species (e.g. swift parrot *Lathamus discolor* and little lorikeet *Glossopsitta pusilla*: NSW Threatened Species Conservation Act 1995). We counted flowers monthly for 24 months at 83 sites, and estimated nectar availability by combining flower-counts with a nectar index derived from the rate at which birds fed on the flowers of different plant species. We modelled nectar availability as a function of mapped environmental variables such as gross primary productivity (derived from satellite telemetry), rainfall and vegetation type. Because many nectarivores inhabit gardens as well as bushland (Catterall 2004, French et al. 2005, Luck et al. 2013), we also measured nectar at eight garden sites. We asked the following questions: (1) what are the temporal and spatio-temporal patterns of nectar availability in the study region, and how much do they differ between years?; (2) which vegetation types and plant species are important sources of nectar?; and (3) which environmental variables influence nectar availability?

Methods

Study region

The 314 400 ha study region is centred on the Bellinger Valley on the mid north coast of New South Wales, Australia, at $152^o 43øE$, $30^o 28øS$ (Fig. 3.1). Elevations range from sea level in the east to c. 1 600 m a.s.l.; the principal topographic feature is a steep escarpment separating the tablelands in the west of the study region from the coastal valleys and ranges. There is a moist subtropical climate with hot, humid summers and warm, drier winters. Temperature maxima in the Bellinger Valley range from 30° C (January) to 20° C (July); minima range from to 18° C (January) to 5° C (July). Rainfall (1,704 mm annually at Coffs Harbour) is highest in summer and

autumn (mean March rainfall is 234 mm) and lowest in winter and spring (mean September rainfall is 61 mm).

Vegetation

Native vegetation persists over 75% of the study region (Fig. 3.1), mainly as large connected blocks. The principal native vegetation type in the study region is sclerophyll forest dominated by *Eucalyptus* spp. , many of which are important sources of nectar for birds. Wet sclerophyll forests (in which the understorey is dominated by fleshy-fruited plants that produce little nectar) occupy 33% of the study region, and dry sclerophyll forests (in which the understorey is not dominated by fleshy-fruited plants) 23%. There are few nectar-producing plants in subtropical or temperate rainforest (12% and 7% of the study region, respectively). ʻWeedy regrowthʼ(1% of the study region) occurs where rainforest has been cleared and subsequently abandoned, and may include nectar-producing species such as silky oak *Grevillea robusta* (Proteaceae) and flooded gum *E. grandis*. Urban areas (4% of the study region) contain gardens and street plantings where nectar-producing species are often abundant (Catterall 2004). The remainder of the study region consists of pasture and farmland, which have little habitat value for nectarivores.

Site selection

We used ArcGIS 9.3 (ESRI) software and a survey gap-analysis procedure (Ferrier et al. 2007) to select 54 sites that sampled the range of native vegetation types and environmental conditions; sites were circular plots of 30-m radius. We located another 18 sites in representative areas of rainforest (the GIS mapping used in site selection did not discriminate between rainforest types) and 11 sites in weedy regrowth, which, at that stage, had not been mapped. Apart from the weedy regrowth sites, all sites

were located in pairs c. 400 m apart; the walk between paired sites allowed us to collect additional data on flowering phenology (results not reported).

Field program

BAH visited each site regularly (usually monthly, sometimes more than once per month) from December 2007 to the end of November 2009, making 1 654 site visits that sampled 1 500 out of a possible 1 992 site-month combinations (24 months × 83 sites). Groups of nearby sites were visited on the same day, but to reduce possible systematic biases we randomized the order in which sites were visited in each group, and the order in which groups were visited in each month. During each 20-min site visit, BAH conducted a 7-min bird survey (results reported in Chapters 4 and 5), then spent 13 min counting flowers (and fruit: results reported in Chapter 2).

Garden sites

We recruited volunteers to count flowers in their gardens by placing advertisements in local newspapers. A circular plot of 30-m radius was located in the garden of each volunteer, and volunteers were instructed in counting flowers. In as many months of the study as possible, each volunteer performed one or more 20-minute surveys of birds and flowers in his or her garden, as described above for bushland sites. Only gardens for which data were available for at least one complete annual cycle were included in analysis; there were eight such gardens ó two surveyed by BAH, and six by volunteers. Six of the gardens were located in rural areas, and two in the town of Bellingen (Fig. 2.1). Garden sites were sampled in 142 out of a possible 192 site-month combinations (24 months × 8 sites).

Estimating nectar

Measuring nectar production directly was not feasible at the scale of our study, so we used estimates derived from flower-counts. For each species in flower during a site visit, we counted the number of plants in flower and estimated the average number of flowers (or inflorescences) per plant. Only species known to provide nectar for birds (Higgins and Davies 1996, Higgins 1999, Higgins et al. 2001, Higgins and Peter 2002) were included in flower counts. A nectar score for each flowering species for each site visit was calculated by multiplying the number of plants in flower by the average number of flowers per plant by a species-specific nectar index. The nectar index (Supplementary Table S2) was derived from data collected between November 2008 and November 2009, during which time we recorded the numbers and species of all birds observed feeding at flowers on-site during surveys. We calculated the nectar index for each flowering species by dividing the total biomass of birds observed feeding on flowers by the total number of flowers recorded between November 2008 and November 2009. Thus, species that attracted greater bird biomass per flower (presumably because they produced more nectar) had a higher nectar index. Nectar scores were summed for all species in flower to give the total nectar score for each site visit. We also calculated nectar scores for ‒reliableø species only; we defined reliable species as those that, in any given year, have at least some individuals in flower ó even though a given individual may not flower in every year. Therefore, we classed swamp mahogany *E. robusta* as a reliable species because, although the plants on-site failed to flower in the first year of the study, plants were observed flowering elsewhere in the study region at this time, and because swamp mahogany was assigned the highest score for flowering regularity by Eby and Law (2008). Where a site was visited more than once in a month, we used the average nectar score for that site-month in analysis.

Environmental variables

Monthly data on rainfall at a 0.05^o grid scale for January 2007 to November 2009 were obtained from the Australian Water Availability Project (http://www.eoc.csiro.au/awap/, accessed 10/11/2010), and were used to derive rainfall totals for periods of periods of 2, 3, 6, 9 and 12 months prior to a given month. Data for mean monthly and annual evapotranspiration rates (0.1^o grid scale) and mean annual potential frost days (0.05^o grid scale) were obtained from the Australian Bureau of Meteorology (accessed 15/10/2010). GIS layers (100-m grid scales) for wetness index, moisture index, annual temperature (mean and minimum), mean annual solar radiation, mean annual rainfall and elevation were obtained from the New South Wales Department of Environment and Conservation. We used ArcGIS 9.3 (ESRI) to derive 100-m grid scale layers for ‒distance from coast‒ and ‒distance from nearest watercourse‒. Data for Gross Primary Productivity (GPP) at 0.0025^o grid scale were obtained from the Australian National University (Berry et al. 2007) on 15/06/2011 and used to derive GPP totals for periods of 6 and 12 months prior to a given month.

Modelling nectar availability

We used Boosted Regression Trees (Elith et al. 2008) to model nectar scores as a function of vegetation type, calendar month and the environmental variables listed above. We built the model using the gbm() package in R (R Core Team 2012) with default learning rate (0.001) and bag.fraction (0.5), maximum interaction depth (5), and 10-fold cross-validation to determine the optimum number of trees. We performed additional 10-fold cross validation on the full model-building procedure (including determination of optimum number of trees) to assess model performance.

We used the fitted model to create 0.0025^o grid maps of predicted nectar scores across the study region for each of the 24 months of the study.

Results

Bushland

More than 50 plant species were recorded flowering in bushland, and most species known to be important sources of nectar for vertebrates flowered at some stage during the study. The species that had the greatest nectar scores (summed over two years) were coast banksia *Banksia integrifolia* subsp. *integrifolia* (21.6% of total nectar score), swamp mahogany (20%, although it was present at only a single site and flowered at that site in only the second year of the study), blackbutt *E. pilularis* (14.9%), flooded gum (11.5%), Sydney blue gum *Eucalyptus saligna* (8.3%), white mountain banksia *Banksia integrifolia* subsp. *monticola* (6.0%), broad-leaved paperbark *Melaleuca quinquenervia* (4.2%), silky oak (3.5%) and pink bloodwood *Corymbia intermedia* (2.4%). Flowers were present in 618 of the 1 500 site-months surveyed, and 78 of the 83 sites had flowers during at least one month of the study.

The Boosted Regression Tree model explained nectar availability reasonably well: the naïve model rank correlation was 0.62, and the mean cross-validation rank correlation 0.20. Four maps of monthly nectar availability (for December 2007, April 2008, December 2008 and April 2009) derived from the Boosted Regression Tree model are presented in Fig. 3.2; these months were chosen to illustrate intra- and inter-annual differences in the spatial distribution of nectar. Gross primary productivity over the previous 12 mo, and rainfall over the previous 6 mo, were the greatest influences on nectar availability (Table 3.1).

Temporal patterns of nectar availability differed between the two years of the study: the only consistent feature was a period of low availability in August and September (Fig. 3.3a). When only reliably flowering species were considered (Table 3.2; Fig. 3.3a), the annual pattern was consistent, with a peak (of differing magnitude) between April and July, a shallow trough in August and September, a small peak in October, and a deep trough from November to January. The temporal pattern of nectar availability was strongly correlated with rainfall over the previous 6 months (Pearson's correlation coefficient = 0.72: Fig. 3.3a).

Between-year differences in nectar availability were mainly caused by the flowering patterns of a few prolific nectar-producing eucalypts (Fig. 3.3b). For example, blackbutt (one of the most abundant trees in the study region) failed to flower in the first summer but flowered well in the second summer (Fig. 3.3b). The sustained period of high nectar availability between April and June 2009 (Fig. 3.3a) was due to heavy flowering by flooded gum, swamp mahogany and, to a lesser extent, winter-flowering blackbutt populations; these taxa had largely failed to flower in the previous year (Fig. 3.3b). Among reliable species, the April-July peak was due to flowering by coast banksia, white mountain banksia and broad-leaved paperbark (Figs. 3b and c), and the October peak (Fig. 3.3a) was attributable to flowering by silky oak (Fig. 3.3c). The April-July peak was greater in the second year because of heavy flowering by swamp mahogany (Fig. 3.3b). Apart from mistletoes (Loranthaceae), no taxa provided nectar in every month of the study.

Patterns of monthly nectar availability among vegetation types differed between years (Fig. 3.4). In the second year of the study, but not the first, nectar availability was high from December to January in wet sclerophyll forest, and from March to July in wet sclerophyll forest, dry sclerophyll forest and subtropical

rainforest. These differences were caused by irregular flowering by eucalypts such as blackbutt, flooded gum and swamp mahogany (a reliably flowering species that flowered only off-site during the first year, but flowered prolifically in the second year at the only site where it occurred).

Gardens

Nectar availability in gardens followed a consistent annual cycle, with a peak between July and October (Fig. 3.5). Shrubby or prostrate members of the genus *Grevillea*, including cultivars, were the most prolific nectar producers (Fig. 3.5); *Banksia* spp. (peak flowering from March to August), *Callistemon* spp. including cultivars (peak flowering in September and October), and the silky oak (peak flowering in October) were also important. Nectar availability in gardens was higher than in bushland (mean nectar score of 528, cf. 63 for bushland).

Discussion

Patterns of nectar availability

Nectar availability in bushland varied widely between months, and at times (e.g. January 2008, August-September 2008 and November 2009) was close to zero. Temporal and spatio-temporal patterns differed between the two years of the study, due mostly to irregular flowering by a few species of eucalypt (e.g. blackbutt, flooded gum, Sydney blue gum). The one consistent temporal pattern was a period of low availability in August and September; this was also identified as a time of scarcity in northern New South Wales by Law *et al*. (2000), and in eastern Australia generally by Eby and Law (2008).

Nectar availability may be thought of as the product of two systems: a ‗reliable‖ system of species that flower every year, and a ‗supplementary‖ system of

irregularly flowering species. Considering only reliably flowering species, temporal patterns of nectar availability in bushland were relatively consistent, with a peak (of differing magnitude) between April and July, a shallow August-September trough, a small peak in October due to flowering by silky oak (a species absent from bushland over much of the study region), and a deep trough from November to January. This pattern suggests that, in years when supplementary species fail to flower, there may be a second, more severe lean season from November to January. This occurred in January 2008, when blackbutt failed to flower and nectar was mostly limited to the comparatively small amounts produced by reliably flowering mistletoes.

The reliable nectar system resulted in some consistent spatio-temporal patterns. In both years, nectar availability was high in coastal areas between April and September (due to flowering by coastal species such as coast banksia and broad-leaved paperbark), and moderate at elevations above 600 m between February and May (due to flowering by montane *Banksia* spp.).

Unlike bushland sites, gardens were dominated by reliably flowering species and followed a consistent annual cycle, with plentiful nectar available throughout the year and a peak (of differing magnitude) between July and October; the peak was largely attributable to flowering by *Grevillea* and *Callistemon* cultivars. Nectar availability in gardens was higher than in bushland (mean nectar score of 528, cf. 63 for bushland), although observer differences mean that this result should be interpreted with caution.

Important nectar-producing species and habitats

Four principal criteria have been used to identify plant species that are important food sources for fauna (Peres 2000, Westcott et al. 2005): reliability; temporal redundancy (i.e. whether a species provides food during times of scarcity); abundance/ubiquity;

and attractiveness to consumers. The flowering season, geographical extent and attractiveness to birds of the reliable nectar-producing plant species in bushland in the study region are described in Table 3.2. Important species under these criteria include coast banksia, white mountain banksia, silky oak, coastal populations of pink bloodwood, and a suite of trees found on poorly-drained sites near the coast: swamp mahogany, broad-leaved paperbark and forest red gum *E. tereticornis*. Most of the important species in Table 3.2 have restricted distributions in the study region, being confined to coastal areas, weedy regrowth and/or higher altitudes. Mistletoes, by contrast, are widespread and, collectively, flower in every month of the year. In many places, mistletoes may be the principal source of nectar (albeit in comparatively small amounts) for months or even years at a time. This accords with previous studies of the value of mistletoes to fauna, both in Australia and globally (Ford et al. 1979, Turner 1991, Watson 2001).

Bushland species that flower reliably during the August-September lean season were mostly restricted to coastal vegetation, which is likely to be an important habitat for nectarivorous birds. Nectar availability in coastal vegetation was high from April to September; these are months of widespread nectar scarcity in eastern Australia (Eby and Law 2008), suggesting that the coastal vegetation in the study region may be a nationally significant source of nectar for migratory and nomadic nectarivores. A decline in nectar in coastal areas between August and October coincided with peak availability in gardens, raising the possibility of a habitat shift from coastal vegetation into gardens at this time. Uniquely among the vegetation types in the study region, gardens produced prolific nectar throughout the year, mainly due to flowering by *Grevillea* cultivars. The nectarivore fauna of some *Grevillea*-rich urban areas is characterized by low diversity (Catterall 2004), but this

was not the case in our study region, where nectarivorous bird diversity in gardens appeared to be high ó possibly because six of the eight garden sites were more or less contiguous with extensive bushland.

Influences on nectar availability

Nectar availability was most strongly influenced by primary productivity and rainfall/water availability: there was generally more nectar at places and times with greater productivity and access to water. Gross primary productivity over the previous 12 mo, and rainfall over the previous 6 mo, were the greatest influences on nectar availability, reflecting the fact that nectar production is the culmination of a process that begins many months or even years prior to flowering (Law et al. 2000). The development of remotely sensed measurements of primary productivity is relatively recent, and we are not aware of any studies that have examined the effect of productivity on flowering or nectar production over large areas. Earlier studies have found that irradiance, temperature, heat sum (i.e. accumulated time above a certain temperature) and rainfall affect community-wide flowering patterns (Smith-Ramirez and Armesto 1994, Wright and Schaik 1994, Diekmann 1996, Fenner 1998, Law et al. 2000, Birtchnell and Gibson 2006); all of these factors are related to primary productivity.

The Boosted Regression Tree model explained most of the spatio-temporal variation in nectar availability. However, we feel that the nectar maps we produced are deficient in some respects. The maps do not show the high nectar availability we observed in coastal vegetation between April and September of both years, when coastal species such as coast banksia, broad-leaved paperbark and swamp mahogany were flowering. We attribute this to the coarseness of the vegetation mapping we used, which made no distinction between coastal sclerophyll vegetation ó a prolific

source of nectar for much of the year ó and non-coastal sclerophyll vegetation, where nectar was generally scarce. The maps appear to over-predict nectar availability in December 2007 and January 2008, when there was very little flowering in bushland, relative to December 2008 and January 2009, when there was widespread flowering by blackbutt, one of the most abundant trees in the region. Our study may have been too brief to accurately estimate the relationships between environmental variables and the irregular flowering patterns of some eucalypts.

Implications for nectarivore strategies

Nectarivorous vertebrates possess two main strategies to cope with variations in nectar availability: diet switching and nectar tracking. Nectarivores can be positioned along a dietary continuum from obligate species (i.e. those that consume only nectar) to those able to subsist for long periods on alternative food types, and along a movement continuum from sedentary species to highly mobile species that track nectar over long distances. The strategies employed by nectarivores, which vary within as well as between species, are likely to be influenced by the spatio-temporal patterns of nectar availability they encounter.

Conditions during our study did not appear to be unusually poor (rainfall was above average in both years), yet there were periods when nectar was almost absent from the bushland in our study region. In the first summer of the study, for example, flowering was largely restricted to mistletoes. Although mistletoes are widespread and flower reliably, they produce little nectar in comparison with species such as eucalypts and banksias, and for ergonomic reasons (Ford and Paton 1985) are unlikely to sustain populations of large nectarivores: we did not observe any species heavier than the Lewinøs honeyeater *Meliphaga lewinii* (37 g) feeding on mistletoe nectar. It would appear that during periods of shortage, when mistletoes are the principal

sources of nectar, the bushland in our study region is incapable of supporting populations of large obligate nectarivores. At these times, species such as wattlebirds *Anthochaera* spp. (68-131 g), friarbirds *Philemon* spp. (67-101 g) and lorikeets (Loriinae: 40-132 g) must either leave the study region, move into gardens (which have limited areal extent and would be unlikely to accommodate substantial proportions of nectarivore populations), or switch to other food types (e.g. insects, fruit or lerps).

Periods of low or zero nectar availability appear to be common features of many Australian ecosystems. Almost all previous studies of community-wide nectar production in Australia have reported severe nectar shortages (e.g. Pyke 1983, Pyke 1985, Collins and Newland 1986, McFarland 1986, Brady 2009). Most of these studies have been conducted over relatively small areas (< 20 km^2); our study demonstrates that nectar shortages may be much more widespread. The implication is that, among Australian nectarivores, a high degree of nectar-obligacy is likely only for species that are small (and therefore able to survive on mistletoes or other relatively meagre nectar sources) and/or highly mobile (i.e. capable of tracking nectar at scales larger than our 300 000 ha study region). ‗Blossom nomads‗(Keast 1967), a characteristically Australian guild of species that track nectar over large scales, probably evolved in response to patterns of nectar availability such as those documented here.

Our results suggest that, among larger nectarivores, sedentary life histories are likely only for species that are able to subsist without nectar for lengthy periods. The recent development of gardens and urban areas that provide prolific nectar throughout the year has altered these patterns, allowing the establishment of some sedentary populations of large species with relatively high degrees of obligacy (e.g. lorikeets:

Shukuroglou and McCarthy 2006). The development of sedentary populations of large, aggressive nectarivores such as lorikeets might have negative effects on smaller nectarivores, such as the eastern spinebill *Acanthorhynchus tenuirostris*.

Competition for pollinators and the evolution of flowering phenologies

Competition for pollinators is an important process driving the evolution of plant phenologies (Levin and Anderson 1970, Waser 1978), and may result in staggered flowering patterns that provide year-round nectar for nectarivores (Stiles 1978, Cotton 2007). However, abiotic factors that constrain nectar production are probably more important in determining flowering patterns at the community level (van Schaik et al. 1993, Smith-Ramirez and Armesto 1994). Community-level nectar production in our study region was largely explained by abiotic factors such as primary productivity and rainfall (which also influences productivity). Although the flowering seasons of bird-pollinated plants showed little sign of the staggered patterns seen in the neotropics (Stiles 1980, Cotton 2007), our results suggest that competition for pollinators may have influenced the phenology of some important nectar-producing species. Assuming that pollinator numbers are relatively constant over time (which appears to be the case in our study region: Chapter 5, Fig. 5.2), then plants that flower during periods of low community-wide nectar availability are likely to achieve greater pollination than plants that flower when nectar is abundant; this might result in evolutionary pressure to flower during periods of scarcity. Periods of scarcity, however, are caused by shortfalls of the resources that plants require to produce nectar (van Schaik et al. 1993), so that flowering at such times may not be physiologically possible, or may reduce a plantøs future reproductive success.

Periods of scarcity appeared to occur when low 6-monthly rainfall limited the capacity of plants to produce nectar. The plant species that produced the most lean-

season nectar all had ¬privilegedø access to water at these times. Important lean season flowering species grew in swampy environments (broad-leaved paperbark, swamp mahogany and forest red gum), near the coast (coast banksia), along creek lines (silky oak), or in gardens (silky oak and *Grevillea* cultivars). Plants in such habitats appear to have good access to water throughout the year; hence, their flowering seasons are unlikely to be constrained by resource availability. That these species flower when nectar is scarce suggests that their flowering phenologies may have been driven by the evolutionary pressure to maximize pollination.

We propose that plants that provide lean-season food for mutualistic consumers are likely to be those with privileged access to the resources that drive temporal cycles of food production. Given that the effect of competition for seed dispersers is likely to be similar to that of competition for pollinators, our hypothesis applies to plant-frugivore mutualisms as well as those between plants and nectarivores. The principal resources driving temporal cycles of production are likely to be light (energy) and water. Plants with privileged access to water and/or light might include species growing in damp environments (e.g. wetlands, streambanks, floodplains and gullies); species growing at the forest edge or in gaps; species of the upper canopy; deep-rooted species; species with high water storage capacity; and species in gardens or agricultural plantings. Many of the plants identified as important sources of lean-season food for nectarivores or frugivores appear to fall into one or more these categories. For example, *Melaleuca* spp. from damp environments are important sources of lean season nectar in northern Australia (Woinarski et al. 2000); *Miconia* plants growing in gaps produce more lean season fruit than conspecifics in the forest interior (Levey 1990); and *Aloe marlothii*, a source of dry season nectar in southern Africa, has a high water storage capacity (Symes et al. 2008).

Table 3.1. Relative influence on nectar availability of variables in Boosted Regression

Tree model (only variables scoring over 5 are shown). Relative influences sum to 100.

Variable	Relative influence
Gross primary productivity (GPP) of previous 12 mo	19.1
Rainfall of previous 6 mo	7.3
Topographic wetness index	7.0
Average annual solar radiation	6.5
Elevation	6.0
Rainfall of previous 9 mo	6.0
GPP of previous 6 mo	5.5
Mean monthly evapotranspiration	5.5
Vegetation type	5.1

Table 3.2. Reliably flowering species (i.e. species of which at least some individuals flower every year) in bushland. Flowering reliability was assessed on the basis of our results and those of Law et al. (2000) and Eby and Law (2008). Mean nectar score per plant is an estimate of the attractiveness to birds of an average individual; it was obtained by multiplying the mean number of flowers/inflorescences on a flowering individual of each species by the nectar index for that species.

Species	Common name	Geographically restricted?	Broad vegetation type	Number of bushland sites	Flowered both years?	Flowering period	Mean nectar score per plant (g of bird per plant in flower)
Grevillea robusta	Silky oak	Restricted to weedy regrowth	Weedy regrowth	1	Yes	October	1102.4
Eucalyptus robusta	Swamp mahogany	Restricted to poorly drained coastal areas	Sclerophyll forest	1	Yes but only off-site	May-Aug	290.1
Banksia integrifolia subsp. integrifolia	Coast banksia	Restricted to coast	Sclerophyll forest	3	Yes	Feb-Oct	129.5
Corymbia intermedia	Pink bloodwood	Widespread; but reliable only near coast	Sclerophyll forest	4	Yes	Jan-Mar	115.7
Melaleuca quinquenervia	Broad-leaved paperbark	Restricted to poorly drained coastal areas	Dry sclerophyll forest	3	Yes	Feb-Jun	22.5

Species	Common name	Distribution	Habitat			Period	
Eucalyptus tereticornis	Forest red gum	Restricted to poorly drained coastal areas	Dry sclerophyll forest	1	Yes but only off-site	May-Sep	15.6
Banksia integrifolia subsp. monticola	White mountain banksia	Restricted to higher altitudes	Sclerophyll forest	7	Yes	Feb-Aug	12.5
Muellerina celastroides	(a mistletoe)	Widespread	Sclerophyll forest	4	Yes	Nov-Feb	6.7
Muellerina eucalyptoides	(a mistletoe)	Widespread	Sclerophyll forest and rainforest	9	Yes	Dec-Mar	6.3
Amyema spp.	(mistletoes)	Widespread	Sclerophyll forest and rainforest	12	Yes	Year round	3.7
Banksia spinulosa	Hairpin banksia	Restricted to higher altitudes	Sclerophyll forest	2	Yes	Apr-Jul	3.3
All mistletoe spp. combined	All mistletoe spp. combined	Widespread	All		Yes	Year round	3.0
Acronychia imperforata	Beach acronychia	Restricted to coast	Rainforest	3	Yes	Mar-Apr	2.5
Syzygium australe	Brush cherry	Widespread	Rainforest and	1	Yes	Mar	1.8

			weedy regrowth				
Eucalyptus microcorys	Tallowwood	Widespread	Sclerophyll forest and weedy regrowth	13	Yes	Jun-Dec	1.8
Elaeocarpus reticulata	Blueberry ash	Widespread	Sclerophyll forest and weedy regrowth	8	Yes but only off-site	Nov-Dec	1.5
Dendrophthoe vitellina	(a mistletoe)	Widespread	Rainforest and wet sclerophyll	9	Yes	Aug-Nov	1.2
Lantana camara	Lantana	Widespread	Sclerophyll forest and weedy regrowth	18	Yes	Year round	1.0
Amylotheca dictyophleba	(a mistletoe)	Widespread	Rainforest and wet sclerophyll	22	Yes	Oct-Feb	0.7
Kennedia rubicunda	Running postman	Widespread	Sclerophyll forest and weedy regrowth	9	Yes	Jul-Dec	0.04

Figure 3.1. Study region, showing locations of survey sites and extent of vegetation cover.

Figure 3.2. Modelled nectar availability across the study region (derived from Boosted Regression Tree model) for (a) December 2007; (b) April 2008; (c) December 2008; and (d) April 2009.

Figure 3.3. Monthly nectar availability: (a) mean nectar score per site (for all species,

and for reliable species only) and mean 6-monthly rainfall; (b) and (c) total on-site nectar scores for the top ten nectar-producing taxa. Because only a few sites were surveyed in March 2009, June 2008 and July 2009, mean nectar values for these months are averages of the months before and after. An exception is March 2008; we didnøt want to omit the data for this month, because there was heavy flowering by Sydney blue gum at two sites, but due to the low number of sites surveyed, the mean nectar score was unrealistically high. We therefore divided the total nectar score for this month by the total number of sites (83), rather than the number of sites surveyed.

Figure 3.4. Total monthly nectar scores for each vegetation type. Temperate rainforest, where nectar availability was always close to zero, has been omitted for clarity.

Figure 3.5. Monthly nectar availability in gardens and bushland, and nectar production by garden *Grevillea* cultivars. Note that bushland is shown on a different scale to gardens and *Grevillea* spp.

Declaration for Thesis Chapter 4

In the case of Chapter 4, the nature and extent of my contribution to the work was as follows:

Nature of contribution	Extent of contribution (%)
I conceived the study, performed all of the fieldwork and 50% of the statistical analyses, and was the primary author of the manuscript.	80%

The following co-authors contributed to the work:

Name	Nature of contribution
Dr Ralph Mac Nally	Ralph Mac Nally contributed ideas to the work and co-authored the manuscript.
Dr James Thomson	James Thomson contributed ideas to the work, assisted with statistical analyses and helped write the ‒statistical analysesø section.

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidateøs and co-authorsø contributions to this work.

Candidateøs Signature		Date
Main Supervisorøs Signature		Date

Chapter 4 How well do frugivorous birds track fruit availability at regional scales?

Abstract

Aim. To document and explain regional patterns of variation in frugivorous bird biomass at multiple spatial and temporal scales.

Location. A 300 000 ha region in subtropical eastern Australia.

Methods. We counted birds and measured fruit at 83 sites monthly for 24 mo. We used Bayesian multi-level analysis of variance (ANOVA) to partition variation in frugivore biomass into spatial (locality, site, vegetation type), temporal (month, season, year) and spatio-temporal components, and to examine the influence of potentially explanatory variables (fruit biomass and diversity, vegetation structure and floristics, and modelled climate) on frugivore biomass.

Results. Fruit biomass and fruiting plant diversity explained much of the variation in frugivore biomass; variables relating to climate and vegetation structure had little additional influence. Most variation was spatial: frugivore biomass was greater in vegetation types, localities and sites with more fruit. Birds moved among localities and vegetation types in response to seasonal changes in fruit availability, but not to the extent warranted by variation in fruit biomass. A lack of purely temporal variation in frugivore biomass suggests that there were no major net movements into or out of the study region. Except for some highly mobile ‑fruit nomads‖, specialist frugivores (i.e. species that feed mainly on fruit) appeared to be more sedentary than generalists.

Conclusions. Food availability was the greatest influence on bird biomass. Birds tracked the spatial distribution of food and, to a lesser extent, its spatio-temporal dynamics. Relatively weak spatio-temporal tracking was probably caused by an over-

supply of food combined with constraints on travel by birds. In the absence of large-scale immigration or emigration, birds were unable to track purely temporal changes in food availability.

Introduction

The availability of resources such as food is a key determinant of the distribution and abundance of organisms. Food availability has been shown to influence the abundance of a range of taxa including invertebrates (Wolda 1978), birds (Karr 1976), mammals (White 2008) and reptiles (Diaz and Carrascal 1991). In a given region, food availability typically varies spatially (e.g. between habitat types: Blake and Loiselle 1991), temporally (e.g. between seasons: Ting et al. 2008), and spatio-temporally (e.g. where the distribution of food across habitat types changes seasonally: Haugaasen and Peres 2005). Ecological theory predicts that such variations will be ‒tracked‒by consumers, such that consumer abundance should be proportional to food availability (Pulliam and Caraco 1984). Many studies have found evidence of some sort of resource tracking (e.g. Levey 1988, Rey 1995), though constraints such as travel costs and imperfect knowledge of food distribution mean that the perfect matching predicted by theory is rarely achieved in natural systems (Kennedy and Gray 1993).

Birds are often used to explore the relationship between food availability and consumer abundance, partly because their mobility allows them to ‒sample‒large areas. Bird abundance has been explained in terms of the availability of foods such as insects (Lefebvre et al. 1994), nectar (Ford and Paton 1985, Cotton 2007) and fruit (Rey 1995, Moegenburg and Levey 2003). Fruit-frugivore mutualisms are particularly important in tropical forests, where around half of the bird biomass is supported by fruit, and up to 90% of tree and shrub species depend on vertebrate frugivores to disperse their seeds (Fleming et al. 1987). Because fruit is patchily distributed in space and time (Fleming et al. 1987), frugivorous birds must either track the changing distribution of fruit across the landscape, or switch to alternative foods during periods

of shortage. Species differ in their use of these strategies: at one extreme are ‑fruit nomads‑ highly mobile specialist frugivores that track fruit over great distances – sometimes > 100 km (Holbrook et al. 2002). Conversely, diet switching allows the persistence of more or less sedentary generalists that eat fruit when available but survive for long periods without it. Some species combine both strategies, diet switching to an extent and tracking fruit over relatively short distances.

Many studies (e.g. Levey 1988, Blendinger et al. 2012) have shown that frugivore abundance in small areas (< 20 km^2) varies in response to fluctuations in fruit availability (i.e. that frugivores track the temporal availability of fruit at small spatial scales). However, studies over small areas can only speculate about where the ‑additional‑ birds may have come from or gone to; a more complete understanding of fruit tracking requires studies at regional or larger scales. Large-scale studies, which have mostly been limited to temperate Europe, have found considerable diversity in patterns of avian fruit tracking. Some species track food strongly, others weakly or not at all (Rey 1995, Telleria et al. 2008). Even within a species, seasonal visitors may track food more closely than territorial residents (Telleria and Perez-Tris 2007). Several authors have noted that tracking is highly dependent on the scale of analysis (Burns 2004, Garcia and Ortiz-Pulido 2004); for example, there appears to be a tendency for closer fruit tracking at large spatial scales (region/landscape) than at smaller ones (locality/habitat patch: Telleria and Perez-Tris 2003, Guitian and Munilla 2008).

Tropical and subtropical forests differ in several important respects from the European ecosystems where most large-scale studies of fruit tracking have occurred. In the tropics and subtropics, fruit is available year-round (Westcott et al. 2005), frugivore biomass is dominated by residents and local migrants (Innis 1989), and fruit

and frugivore communities are highly diverse (Fleming et al. 1987). In Europe, by contrast, fruit is available for only part of the year (Telleria and Perez-Tris 2003), long-distance migrants are prominent (Rey 1995), and there are relatively few species of fruiting plants and frugivores (Telleria et al. 2008). Despite their importance to frugivores, there have been few studies of fruit tracking over large areas in tropical or subtropical forests.

We examined fruit tracking by birds at multiple spatial and temporal scales over 24 months across a 300 000 ha region in subtropical eastern Australia. The study region provides habitat for many frugivorous birds, including several rare and threatened species (e.g. wompoo fruit-dove *Ptilinopus magnificus*, rose-crowned fruit-dove *P. regina*, superb Fruit-dove *P. suberba* and barred cuckoo-shrike *Coracina lineata*: New South Wales Threatened Species Conservation Act 1995). We counted birds and measured fruit monthly at 83 sites, then partitioned variation in frugivore biomass into spatial, temporal, and spatio-temporal components, and examined the influence of fruit availability on each component. We addressed the following questions: (1) what are the spatial, temporal and spatio-temporal patterns of frugivore biomass?; (2) are these patterns influenced by food availability (i.e. do frugivores track fruit)?; and (3) do the patterns differ between feeding guilds (generalists, specialists and ‑fruit nomadsø)? Although many studies of resource tracking have not considered the effects of other factors, food is unlikely to be the only variable influencing consumer distributions (Herrera 1998); for example, weather and vegetation structure may also affect frugivore abundance (Boyle et al. 2010, Crampton et al. 2011). We therefore asked: (4) what other factors influence frugivore biomass?

Methods

Study region

The 314 400 ha study region is centred on the Bellinger Valley on the mid north coast of New South Wales, Australia, at $152^o\,43$øE, $30^o\,28$øS (Fig. 4.1). Elevations range from sea level in the east to c. 1 600 m a.s.l. There is a moist subtropical climate with hot, humid summers and warm, drier winters. Temperature maxima in the Bellinger Valley range from 30° C (January) to 20° C (July); minima range from to 18° C (January) to 5° C (July). Rainfall (1,704 mm annually at Coffs Harbour) is highest in summer and autumn (mean March rainfall is 234 mm) and lowest in winter and spring (mean September rainfall is 61 mm).

Vegetation

Native vegetation persists over 75% of the study region (Fig. 4.1), mainly as large connected blocks. The principal vegetation type in the study region is sclerophyll forest dominated by *Eucalyptus* spp.; these produce woody fruits that are not eaten by frugivorous birds. Wet sclerophyll forests (in which the understorey is dominated by fleshy-fruited plants) occupy 33% of the study region, and dry sclerophyll forests (in which fleshy-fruited plants are absent or uncommon) 23%. Subtropical rainforest (12% of the study region) has a complex structure and high diversity of trees; temperate rainforest (7%) has fewer vines, lianas and epiphytes, few or no large figs, and lower tree diversity. ÷Weedy regrowthø (1%) occurs where rainforest has been cleared and the land has later been abandoned; it often includes high densities of exotic species such as camphor laurel *Cinnamomum camphora*. The remainder of the study region consists of pasture and farmland, which have little habitat value for frugivores, and urban areas, which may include fleshy-fruited plant species.

Site selection

We used ArcGIS 9.3 (ESRI) software and a survey gap-analysis procedure (Ferrier et al. 2007) to select 54 sites that sampled the range of native vegetation types and environmental conditions; sites were circular plots of 30-m radius. We located another 18 sites in representative areas of rainforest (the GIS mapping used in site selection did not discriminate between rainforest types) and 11 sites in weedy regrowth, which at that stage had not been mapped. Apart from the weedy regrowth sites, all sites were located in pairs c. 400 m apart; the walk between paired sites allowed us to collect additional data on fruiting phenology (results not reported).

Field program

BAH visited each site regularly (usually monthly, sometimes more than once per month) from December 2007 to the end of November 2009, sampling 1 500 out of a possible 1 992 site-month combinations (24 months × 83 sites). Groups of nearby sites were visited on the same day, but to reduce systematic biases we randomized the order in which sites were visited in each group, and the order in which groups were visited in each month. During each 20-min site visit BAH conducted a 7-min bird survey, then spent 13 min counting fruit (and flowers: results reported in Chapter 3).

Measuring fruit

For each species in fruit during a site visit, we counted the number of plants fruiting and estimated the average number of full-sized fruits per plant. Only fruits known to be eaten by birds were included in calculations of fruit biomass. For species whose full-sized fruits change colour as they ripen (e.g. camphor laurel, giant pepper vine *Piper novaehollandiae* and brown beech *Pennantia cunninghamii*), we classed fruit as

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either ripe or unripe. Fruit biomass for each fruiting species was calculated by multiplying the number of plants in fruit by the average number of fruits per plant by the average wet fruit mass; the latter data were obtained by weighing × 20 fruits of each species in the field using a handheld spring balance. Fruit biomass was summed for all fruiting species to give the total fruit biomass for each site visit. Unripe camphor laurel fruits, which were seldom eaten in relation to their abundance, were excluded from measurements of fruit biomass. Where a site was visited more than once in a month, we used the average fruit biomass for that site-month in analyses. We also recorded the number of species in fruit for each site-month, and calculated the total number of fruiting species at each site and locality (localities were circles of 2-km radius) summed over the two years of the study. To estimate the ‒severity‖of the lean season, we calculated the minimum three-month fruit biomass (measured over three consecutive months, excluding site-months for which we lacked data) for each site.

Bird surveys

We (BAH undertook all surveys) conducted a 7-min point count of birds at the commencement of each site visit. Each time birds were seen or heard, we noted the species and number of individuals, and used a laser range-finder to estimate the distance of the birds from the centre of the site. At the end of each 7-min count, we recorded the total number of individuals of each bird species that had occurred on-site. For example, if there were two Lewin's honeyeaters *Meliphaga lewinii* at a site at the beginning of a count; if these birds left the site during the count; and if another Lewin's honeyeater came onto the site during the count, then the total number of Lewin's honeyeaters recorded at the site for that count was three. All bird counts commenced within 5 hr of sunrise. For each count, we recorded shade temperature,

estimated the percentage of the canopy in sunlight, and scored cloud cover, wind, rain and noise on a scale of 0-4 (low to high). Data from bird counts conducted in noisy conditions (65 surveys where noise was 3 or 4 as a result of strong winds or singing cicadas) were discarded. For each site visit, we calculated the biomass of each species as follows: biomass = total number of individuals recorded on-site during count $\times$ average mass of an individual of that species (based on data in Higgins and Davies 1996, Higgins 1999, Higgins et al. 2001, Higgins and Peter 2002, Higgins et al. 2006). We summed the biomass of all frugivorous species recorded during a site-visit to obtain the total frugivore biomass. Where a site was visited more than once in a month, we used the average frugivore biomass for that site-month in analyses

Guild classifications

Birds were classified as frugivores or not using published data (Holmes 1987, Innis 1989, Higgins and Davies 1996, Church 1997, Higgins 1999, Higgins et al. 2001, Higgins and Peter 2002, Higgins et al. 2006, Floyd 2008) and field observations: where fruit was judged a substantial part of a bird $ø$s diet, the species was classified a frugivore (Supplementary Table S3). Frugivores were assigned to feeding guilds (generalists, specialists and fruit nomads) based on a combination of published material (Holmes 1987, Innis 1989, Higgins and Davies 1996, Church 1997, Higgins 1999, Higgins et al. 2001, Higgins and Peter 2002, Higgins et al. 2006, Floyd 2008) and our own observations during the study (Supplementary Table S3). Specialist frugivores are species that rely heavily on fruit for food; generalists are species that are less reliant on fruit. -Fruit nomadsø are a sub-guild of specialist frugivores comprising species known to travel widely in search of fruit. We use the terms ÷generalistø and ÷specialistø, rather than the usual ÷obligateø and ÷facultativeø frugivores, because many specialist species eat other foods on occasion, and one

(white-headed pigeon *Columba leucomela*) may eat substantial quantities of seed. However, during the study we did not observe this species eating seed in natural areas, except beneath camphor laurel trees whose fruits were also an important part of its diet, and we therefore classified it as a specialist.

Vegetation variables

Vegetation variables were measured between April and August 2010; there was little evident seasonal variation. Variables were measured within a circle of 15-m radius around the centre of each site, after checking that results obtained this way were consistent with results obtained from measuring the entire (30-m radius) site in a pilot study (results not reported). We assigned each site to a vegetation type, which took precedence over the mapped vegetation type if there was a conflict. Canopy height was measured at the centre of each site with a laser range-finder. Trees were counted, identified to species and classed as saplings (< 10 cm diameter at breast height [DBH]), small (10-25 cm DBH), small-medium (25-40 cm DBH), medium (40-60 cm DBH), large (60-80 cm DBH) or very large trees (>80 cm DBH). Exact DBHs were recorded for all trees with DBH $\times$ 40 cm. The numbers of liana (woody vine) stems, trees with basal hollows, trees with hollow-bearing limbs, stumps and dead trees were counted, and the volume and biomass of fallen logs calculated, using a mean density of 0.6 t m^{-3} for fallen timber (Mac Nally et al. 2002). Above-ground plant biomass estimates were derived using the general allometric equations for rainforest and eucalypt forest vegetation types given on page 70 of Keith et al. (2000). Five 2.5 m $\times$ 2.5 m quadrats were randomly located at each site, within which ground cover (percentage leaf litter, vegetation, rock and bare ground), percentage cover of vegetation < 2 m, Leaf Area Index (measured using a CI-130 Digital Plant Canopy Imager: CID Bio-Science), and plant species richness were recorded.

Environmental variables

Monthly data on rainfall, temperature maxima and solar exposure at a 0.05^o grid scale for January 2007 to November 2009 were obtained from the Australian Water Availability Project (http://www.eoc.csiro.au/awap/, accessed 10/11/2010), and were used to derive rainfall totals for periods of 2, 3, 6, 9 and 12 months prior to a given month. Data for mean annual rainfall (0.025^o grid scale), mean monthly and annual evapotranspiration rates (0.1^o grid scale), mean monthly and annual numbers of frost days (0.05^o grid scale), annual temperature (mean, maximum and minimum: 0.025^o grid scale), mean and minimum monthly temperature (0.025^o grid scale), mean monthly and annual sunshine hours (0.025^o grid scale), and mean monthly and annual solar exposure (0.05^o grid scale) were obtained from the Australian Bureau of Meteorology on 15/10/2010. GIS layers (100-m grid scales) for wetness, annual temperature (mean, maximum and minimum), mean annual solar radiation, slope, moisture index, mean rainfall of driest quarter, mean annual rainfall, elevation and aspect were obtained from the NSW Department of Environment and Conservation. We used ArcGIS 9.3 (ESRI) to derive 100-m grid scale layers for ÷distance from coastø and ÷distance from nearest watercourseø Data for Gross Primary Productivity (GPP) at 0.0025^o grid scale were obtained from the Australian National University (Berry et al. 2007) on 15/06/2011 and used to derive GPP totals for periods of 2, 3, 6, 9 and 12 months prior to a given month.

Statistical analyses

We used Bayesian multi-level analysis of variance (ANOVA) (Gelman 2005, Qian and Shen 2007) to partition variation in fruit biomass and frugivore biomass into spatial and temporal components, and to examine the relationship between frugivore biomass and fruit at multiple spatial and temporal scales. Bayesian multilevel

ANOVA uses hierarchical regression models to partition variation in response variables among sources of variation (Gelman 2005, Qian and Shen 2007). The basic model may be expressed as:

$$y_i = \alpha + \sum_{s=1}^{S} \beta_{l_i}^s + \varepsilon_i$$

model (1)

In model (1), α is the grand mean, the βs are linear coefficients corresponding to group level effects (deviations from conditional means) within each of S sources of variation (factors), and ε_i is the residual error. $\beta_{l_i}^s$ is the coefficient for level l (e.g. sclerophyll forest) of factor s (e.g. vegetation type) relevant to datum i. The coefficients within each source s were drawn from exchangeable normal prior distributions, $\beta_l's \sim Normal(0, \sigma_l s'2$) with the corresponding standard deviations assigned flat uniform priors, $\sigma_s \sim Uniform(0, maxsd)$, where $maxsd$ was >> SD(y). The variance component for factor s is estimated by σ_s^2 (the ÷supra-populationø variance) or by the variance of the coefficients, var(β^s) (the ÷finite-populationø variance: Gelman 2005). We used the latter measure because it is more stable for factors with few sampled levels, and more relevant when all levels of interest have been sampled (e.g. vegetation type). The two measures are essentially equivalent for factors with many levels.

The spatial components in our models were site, locality and vegetation type (hereafter vegtype), and the temporal components were month [1-24], season, year and season $\times$ year (among-year variation in seasonal patterns). We also included 4 spatio-temporal terms: site $\times$ season, locality $\times$ season, vegtype $\times$ season and vegtype $\times$ year. Other interaction terms, including 3-way interactions, generally had near-zero variance components in initial model fitting, and were excluded from final models. Localities were groups of sites within a 2-km radius; we arrived at this distance after

trialling various radii from 500 m to 5 km, and finding that 2 km was the smallest

radius that resulted in clear differences between the effects of locality and site.

÷Seasonørepresented fruiting seasons based spatial patterns of fruit availability at

different times of year. The four seasons were: Giant Pepper Vine (December and

January); Bangalow (February and March); Camphor Laurel (April to August); and

Acronychia (September to November).

To examine the association between frugivore biomass and fruit biomass, we

added spatial and temporal components of fruit biomass as covariates to models of

frugivore biomass. The spatial fruit covariate was the mean fruit biomass over 24

months at each site ($\overline{f_s}$). The temporal fruit covariate was the deviation from the site-

specific mean in each survey ($f'_{sm} = f_{sm} - \overline{f_s}$). We assessed how much variation in

frugivore biomass was explained by fruit at each spatial and temporal scale by

comparing the variance components in models with and without fruit covariates. We

also used Bayesian model selection, implemented with reversible jump MCMC (Lunn

et al. 2009, Thomson et al. 2010), to assess the influence of a range of additional

variables on frugivore biomass. Bayesian model selection uses Bayes factors (ratios of

marginal likelihoods) to weight model structures (combinations of variables), and

yields model-averaged regression coefficients and posterior probabilities that each

variable is a predictor (has non-zero coefficient: Wintle et al. 2003, Thomson et al.

2007). The set of additional candidate predictors was derived from expert knowledge

and literature (Ferrier et al. 2002), and included climate, vegetation, and landscape

contextual variables (Table 4.2). Landscape fruit availability was estimated by using

Boosted Regression Trees (Elith et al. 2008) to model fruit biomass for each site-

month as a function of vegetation type, calendar month and the environmental

variables listed above, then mapping predicted fruit biomass at a resolution of

0.0025^o. We built the Boosted Regression Tree model using the gbm() package in R (R Core Team 2012) with default learning rate (0.001), bag.fraction (0.5), maximum interaction depth (5), and 10-fold cross-validation to determine the optimum number of trees. To calculate landscape fruit availability for each month, we summed, for each grid cell in the study region, the mapped values of predicted fruit biomass within 5 grid cells, excluding grid cells where vegetation type was mapped as cleared (where fruit availability was effectively zero) or urban (for which we lacked fruit availability data).

The full model relating frugivore biomass to fruit biomass and additional covariates was:

$$y_i = \alpha + \sum_{s=1}^{S} \beta_{l_i}^s + \beta_1^f \cdot \overline{f_{s_i}} + \beta_2^f \cdot f'_{sm_i} + \sum_{j=1}^{Q} \gamma_j x_{i,j} + \varepsilon_i$$ model (2)

In model (2), the β^fs are the linear coefficients associated with the spatial and temporal components of fruit biomass, the γs are model averaged linear coefficients associated with Q additional candidate covariates, and the remaining parameters are as defined in model (1).

Exploratory modelling indicated that –number of species in fruitø(ranging from 0-8) and –fruit biomassøwere equally important influences on frugivore biomass. We chose –fruit biomassøas our primary covariate because we considered it biologically plausible that fruit biomass should be the main determinant of frugivore biomass. Because fruit nomads appeared to be influenced by landscape fruit availability, we ran models (1) and (2) for fruit nomads with –modelled fruit availability within 5 grid cellsøas the main covariate, and –fruit biomass measured on-siteøreplacing it as an additional candidate covariate.

All models were estimated by Markov chain Monte Carlo with WinBUGS software (v. 14: Lunn et al. 2000) using the reversible jump add-on (Lunn et al. 2009) for model selection and spline fitting. Parameter posterior distributions were sampled over 3 independent chains of 50000 iterations each, after 20 000 iteration burn in periods. Examination of chain histories and BGR diagnostics confirmed that adequate MCMC mixing and convergence were achieved. We used ˗raw˗ measurements of bird counts, because attempting to account for detection error may produce biases at least as great as the biases that arise when detection eror is ignored (Welsh et al. 2013). Response variables and covariates with skewed distributions were log-transformed.

Results

Fruit biomass

Approximately one third (37.4%) of the variation in fruit biomass was partitioned into spatial components (site, locality and vegtype), 25.6% into spatio-temporal components (the site × season, locality × season, vegtype × season and vegtype × year interactions) and 6.7% into temporal components (month, season, year and the season × year interaction) (Fig. 4.2); 30.3% (the residual in Fig. 4.2) could not be partitioned. Vegetation type (which accounted for 25.7% of the variation in fruit biomass) was the largest single component, followed by site (8.1%) and the vegtype × season (8.0%), vegtype × year (7.0%), site × season (5.4%) and locality × season (5.2%) interactions (Fig. 4. 2): fruit biomass was greater in certain vegetation types (particularly weedy regrowth and subtropical rainforest) and at certain sites; there were seasonal changes in the distribution of fruit among vegetation types (Fig. 4.3a), sites and localities; and the distribution of fruit among vegetation types differed between the two years of the study.

Frugivore biomass

Twenty-four species of frugivorous birds were recorded during the surveys. Specialist frugivores comprised 35% of the total frugivore biomass, and generalist frugivores 65%. Fruit nomads, a sub-guild of specialist frugivores, comprised 15% of the total frugivore biomass; fruit nomad biomass was dominated by the topknot pigeon *Lopholaimus antarcticus* and white-headed pigeon. Long-distance migrants (i.e. species where most or all of the population leaves the study region for part of the year) comprised 0.42% of frugivore biomass. The species that contributed the most biomass were Australian brush-turkey *Alectura lathami* (20.9%), Lewin's honeyeater (10.0%), brown cuckoo-dove *Macropygia amboinensis* (9.7%), topknot pigeon (8.5%), wompoo fruit-dove (8.5%) and Australian king-parrot *Alisterus scapularis* (8.0%). Frugivores were present in 794 of the 1 435 site-months used in analysis, and every site had frugivores during at least one month of the study. The mean frugivore biomass per site-month was 244 g; the maximum was 6.0 kg.

Approximately a third (30.5%) of the variation in combined frugivore biomass was partitioned into spatial components (site, locality and vegtype), 5.3% into spatio-temporal components (the site × season, locality × season, vegtype × season and vegtype × year interactions) and 2.6% into temporal components (month, season, year and the season × year interaction) (Fig. 4.2); 61.6% (the residual in Fig. 4.2) could not be partitioned. Vegetation type (which accounted for 18.1% of the variation in biomass) was the largest component of variation (Fig. 4.2), with biomass being greatest in weedy regrowth and subtropical rainforest. Site (5.4%) and locality (7.0%) were also important (Fig. 4.2). The locality × season (1.6%) and vegtype × season (2.8%) interactions imply a degree of seasonal movement between localities and vegetation types: there appeared to be a transfer of frugivore biomass between

subtropical rainforest (in Bangalow season) and weedy regrowth (in Camphor Laurel season: Fig. 4.3b).

The distribution of frugivore biomass differed among guilds (Fig. 4.4). The pattern for generalist frugivores (Fig. 4.4a) was similar to the overall pattern, whereas specialist frugivores (Fig. 4.4b) exhibited less spatio-temporal variation than other guilds. Fruit nomads (Fig. 4.4c) differed from other guilds in two ways: (1) their biomass varied little among sites (but greatly among localities); and (2) they were strongly affected by the locality × season interaction, implying substantial seasonal movements between localities.

Fruit tracking

For combined frugivores, fruit biomass accounted for 20.2% of the variation in bird biomass (Table 4.1). Fruit explained most of the variation in bird biomass between vegetation types and localities, and a substantial proportion of the variation attributable to the locality × season interaction (Fig. 4.2 and Table 4.1). Fruit biomass explained a small proportion (17.7%) of the vegtype × season interaction, suggesting that seasonal movements by frugivores between vegetation types were only partly driven by fruit tracking.

The inclusion of additional covariates increased the explanatory power of the model to 26.3% (Table 4.1); covariates relating to fruiting plant diversity (‗number of species in fruit at a siteø and ‗total number of fruiting species at a site [summed over 2 years]ø) were supported for inclusion as predictors, but covariates relating to climate and vegetation structure were not (Table 4.2).

To determine whether the influence of ‗number of species in fruit at a siteø might be a function of the number of individual plants in fruit, and whether the influence of ‗total number of fruiting species at a site (summed over 2 years)ø might

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be a function of the greater duration of fruiting at sites with greater fruiting plant diversity, we ran the model with ‑number of individual plants in fruit at a site‑and ‑proportion of surveyed months in which a site had fruit‑as additional candidate covariates. Probabilities of inclusion were: ‑number of species in fruit at a site‑0.99; ‑number of individual plants in fruit at a site‑0.21; ‑total number of fruiting species at a site (summed over 2 years)‑0.80; and ‑proportion of surveyed months in which a site had fruit‑0.73. These results suggest that the number of individual plants in fruit was not responsible for the influence on bird biomass of ‑number of species in fruit at a site‑, and that fruiting duration was not solely responsible for the influence on bird biomass of ‑total number of fruiting species at a site (summed over 2 years)‑.

The nature of fruit tracking differed among frugivore guilds. The explanatory power of fruit availability decreased with decreasing guild size (in terms of percentage of total frugivore biomass): combined frugivores tracked fruit most strongly, followed by (in descending order) generalists, specialists and fruit nomads (Table 4.1). The pattern of fruit tracking for generalist frugivores was similar to the overall pattern, with the difference that generalists appeared to be more influenced by landscape fruit availability (‑modelled fruit availability within 5 grid cells‑) than combined frugivores (Table 4.2). For specialist frugivores, fruit biomass explained most of the variation in bird biomass between sites, but only a relatively small proportion of variation between localities and vegetation types (Table 4.1). Variation between localities and vegetation types for specialist frugivores was largely explained by two additional covariates: ‑number of species in fruit at a site‑and ‑above-ground plant biomass‑(Tables 1 and 2). For fruit nomads, the main components of variation (locality and the locality $\times$ season interaction) were only partly explained by fruit (Table 4.1). However, when we modelled fruit nomad biomass as a function of

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landscape fruit availability (modelled fruit biomass within 5 grid cells = 1.275 km), the proportion of variation in these components explained by fruit increased substantially (Table 4.1), suggesting that the preference of fruit nomads for particular localities, and particular localities in particular seasons, is determined more by landscape- than by site-scale fruit availability. Besides fruit biomass, fruit nomads were influenced by 'number of species in fruit at a site', 'total number of fruiting species at a site [summed over 2 years], and 'above-ground plant biomass' (Table 4.2).

To determine whether the influence of 'above-ground plant biomass' on the biomass of specialist frugivores and fruit nomads was due to a preference for the types of fruit produced in vegetation with high above-ground plant biomass, we ran the model for specialist frugivores with 'specialist fruit biomass' instead of 'fruit biomass', and for fruit nomads with 'fruit nomad fruit biomass' instead of 'fruit biomass', including in our fruit biomass calculations only those fruits known to be eaten by specialist frugivores and fruit nomads, respectively. The probability of inclusion of 'above-ground plant biomass' in these models was 0.98 for specialists and 0.69 for fruit nomads. This suggests that the types of fruit available were not responsible (in the case of specialists), or partly responsible (in the case of fruit nomads), for the preference for sites with high above-ground plant biomass.

All guilds exhibited stronger spatial than temporal fruit-tracking (Table 4.3). At the site-scale, the slope of the line of best fit for spatial tracking by combined frugivores was 1.5 cf. 0.5 for temporal tracking (Fig. 4. 5a, b).

Discussion

Patterns of frugivore biomass

Most of the variation in combined frugivore biomass was spatial: biomass differed among (in descending order of importance) vegetation types, localities (circles of 2-km radius) and sites (circles of 30-m radius). There was some spatio-temporal variation in frugivore biomass, mainly in the form of seasonal movements between vegetation types and, to a lesser extent, localities. There was little purely temporal variation in combined frugivore biomass, suggesting that there were no major population fluctuations or net movements into or out of the study region. The birds recorded included several summer migrants (e.g. rose-crowned fruit-dove and barred cuckoo-shrike), but these accounted for < 1% of frugivore biomass. The lack of temporal variation suggests that most movements by frugivores were confined within the study region, and that the scale of our study was equal to or greater than the scale at which birds used the landscape.

Some of the variation in frugivore biomass may have been caused by variation in detectability: birds may have been more detectable in certain vegetation types, at certain seasons, or at certain values of food availability (for example, birds may have been noisier where fruit was more abundant). However, this problem is not easily tractable: attempting to account for detection error may produce biases at least as great as the biases that arise when detection error is ignored (Welsh et al. 2013).

Influences on frugivore biomass

Fruit biomass explained 20.2% of the variation in biomass for combined frugivores, and was an important determinant of the preference of frugivores for certain vegetation types and localities (Table 4.1); variables relating to vegetation structure and broad-scale climate, by contrast, had little additional influence on combined frugivore biomass (Table 4.2). The proportions of variation in bird biomass explained by fruit (Table 4.1) are likely to be underestimates, because the biomass values for

most site-month combinations were derived from only a single 7-minute bird count, and so were highly susceptible to stochastic variability arising from the small-scale, short-term comings and goings of birds (the residuals in Figs. 4.2 and 4.4).

Frugivore biomass was influenced by fruiting plant diversity as well as fruit biomass: bird biomass was greater when there were more plant species in fruit at a site, and at sites with more fruiting plant species (summed over two years). A possible explanation is that frugivores benefit from dietary variety (Herrera 1985), and that a site with, say, 500 g of fruit divided between two fruiting species is more attractive than a site with the same amount of fruit provided by a single species.

Differences between guilds

Specialist frugivores (i.e. birds whose diets consist mainly of fruit) exhibited less spatio-temporal variation than generalists. This pattern might have resulted because specialists were more sedentary than generalists, or because individual specialists made opposite seasonal movements that resulted in little net spatio-temporal variation. The latter explanation appears unlikely, and we interpret our findings as evidence that specialist frugivores were more sedentary than generalists. Another difference between the two guilds was that specialists were influenced not only by fruit, but also by vegetation structure, preferring localities and vegetation types with greater above-ground plant biomass (hereafter called ‗big forests‖). This preference, which was not related to the type or amount of fruit available in big forests during the study, might have arisen if specialists were physiologically adapted to cooler, shadier conditions. Alternatively, big forests might be more reliable sources of fruit during periods of scarcity: being relatively sedentary, specialists may prefer localities and vegetation types that provide food even in unusually poor seasons.

That generalists moved more than specialists was surprising. We expected that specialists, with their greater reliance on fruit, would need to track spatio-temporal fruit availability closely, whereas generalists, which have the option of switching to other food sources when fruit is scarce, would be more likely to remain in a single location. One explanation for the greater mobility of generalists is that alternative food sources (e.g. invertebrates and nectar) may themselves be subject to pronounced spatio-temporal variation, inducing movements that are not related to fruit availability. A second explanation is that generalists may eat a more restricted range of fruits than specialists (Schleuning et al. 2011), in which case they might need to move further to find preferred food plants.

Fruit nomads, a sub-guild of specialist frugivores, exhibited much greater spatio-temporal variation than other guilds, moving seasonally between localities and ó to a lesser extent ó sites and vegetation types. These movements were better explained by landscape fruit availability (modelled fruit within a radius of c. 1.275 km) than by on-site fruit biomass, suggesting that fruit nomads tracked fruit at larger scales than other guilds.

Effects of variation in detectability

Our results may have been affected to some degree by variation in detectability: birds may have been more detectable in certain vegetation types, at certain seasons, or in certain weather conditions. We did not attempt to account for detection error, because such attempts may produce biases at least as great as the biases that arise when detection error is ignored (Welsh et al. 2013). Several lines of reasoning suggest that the effect of variations in detectability is likely to have been minor compared with the effect of genuine variations in biomass. First, when we modelled frugivore abundance as a function of two important variables that affect detectability (background noise

and percentage sunlight on canopy), the explanatory power of the model was low relative to models that incorporated food availability, vegetation, or – to a lesser extent – climate (Chapter 6, Table 6.1). Second, above-ground plant biomass (which might be expected to affect detectability, with birds being more difficult to detect in denser vegetation) had a low probability of inclusion in models of frugivore biomass, except for specialist frugivores and fruit nomads, where its effect was positive (i.e. biomass was greater in denser vegetation: Table 4.2). Third, we found that bird abundance (for all birds, not just frugivores) was greatest in the densest vegetation types (weedy regrowth, subtropical rainforest and wet sclerophyll forest: Chapter 6, Fig. 6.3) – whereas, if detectability were the dominant influence on observed patterns of bird abundance, then abundance would be greatest in more open vegetation types (e.g. dry sclerophyll forest).

Resource tracking in space and time

Ecological theory predicts a perfect match between resources and consumers, such that spatio-temporal variation in the distribution of resources results in equivalent variation in consumer abundance (Pulliam and Caraco 1984). Contrary to this prediction, we found that frugivores were rather sedentary, tending to remain in vegetation types and localities that had higher mean fruit biomass; they did not move around to the extent that might have been expected, given the degree of spatio-temporal variation in fruit availability (Table 4.3, Fig. 4. 5).

One implication is that fruit must have often been non-limiting during our study. In a situation where birds were limited by food, a reduction food availability would force them to travel or else starve; either outcome would result in spatial and temporal tracking of equal strength. But in a situation where food was non-limiting, a reduction in food availability would not force any birds to travel or to starve. This

would result in the observed pattern of stronger spatial than temporal resource tracking.

Why should fruit have been non-limiting? Fluctuating resources are thought to limit bird populations during periods of scarcity ('bottlenecks': Wiens 1977, 1989). Ecological bottlenecks may be regular seasonal phenomena or, in the case of resources that fluctuate supra-annually, they may occur at intervals of a decade or more (Wiens 1977, 1989). We found no evidence that frugivore biomass was limited by fruit bottlenecks during our study; however, inter-annual differences in fruit availability may mean that bottlenecks limit populations only in particularly poor years. Data from Australia are lacking, but marked annual variations have been observed in long-term studies in other parts of the world; for example, year-to-year fruit supply varies 14-fold in Spain (Herrera 1998) and eight-fold in Borneo (Fredriksson 2006). Rainfall, a correlate of productivity and fruit abundance (Ting et al. 2008), was above average during the study (1,738 to 2,347 mm p.a. at Coffs Harbour, cf. the annual mean of 1,704 mm), but there had been below average rainfall between 2000 and 2007 (1,090 mm in 2003 was the lowest annual total since 1968). Fruit would have been generally in over-supply during our study if frugivore populations had been limited by, and had not yet recovered from, earlier periods of drought-induced shortage. An alternative possibility is that biotic interactions such as predation and parasitism might have prevented frugivore populations from reaching carrying capacity (Andrewartha and Birch 1954).

If bird fitness increases as the ratio of resource availability to bird biomass increases (which seems likely: Shochat et al. 2002), then even where food is non-limiting, the observed pattern of stronger spatial than temporal tracking would develop only if there were constraints on the capacity of birds to travel. There are

several reasons why birds might be reluctant or unable to move across the landscape. Travel is energetically costly; breeding birds cannot move far from their nests; some species are territorial; and movements outside of a well-known area are likely to result in decreased foraging efficiency and increased predation risk. Also, given that birds lack perfect knowledge of resource distribution (Kennedy and Gray 1993), there is no guarantee that travel will lead a bird to an area with more food.

Given that constraints on travel are likely to apply to many or even most birds, and that food availability is likely to limit consumer populations only occasionally, stronger spatial than temporal resource tracking may be the norm in closed systems (i.e. those without major influxes or effluxes of consumers). In such systems, the strength of temporal tracking should increase as resources become scarce, or when constraints on movement are relaxed (e.g. outside the breeding season, or among non-breeding migrants). This is supported by Telleria and Perez-Trisø (2007) finding that frugivorous birds in Spain exhibited stronger spatial than temporal tracking, but that temporal tracking was much stronger among over-wintering migrants than among resident birds.

Comparisons with other studies

The few previous multi-year, multi-scale studies of regional food tracking have investigated fruit-frugivore systems in temperate Europe (Telleria and Perez-Tris 2007, Guitian and Munilla 2008, Telleria et al. 2008); this study is among the first to examine regional food tracking in the tropics or subtropics, the zones where most frugivores live. There were some broad similarities between our findings and those from Europe. For example, birds tracked food in both systems, and in both systems there was a tendency for stronger tracking at larger spatial scales, although the

discrepancy between locality- and site-scale tracking in our study was not as marked as those reported by Telleria and Perez-Tris (2003) or Guitian and Munilla (2008).

Some important differences between our findings and those from Europe can be attributed to differences in the proportion of migrants: long-distance migrants are the dominant frugivores in many European systems, but comprised < 1% of the biomass in our study region. Migratory birds are less constrained in their ability to travel than residents, allowing them to track spatio-temporal changes in food availability more closely. Birds in Europe tracked temporal changes in food availability, at least to some extent (Guitian and Munilla 2008, Telleria et al. 2008), whereas temporal tracking was very weak in our study region. Similarly, the only European study to have compared spatial and temporal tracking at the site-scale (equivalent to our Fig. 4.5) found that, in habitats dominated by over-wintering migrants, temporal tracking was almost as strong as spatial tracking (Telleria and Perez-Tris 2007; the slope of temporal tracking was 83% of the slope of spatial tracking, cf. 33% in our study). The greater degree of temporal and spatio-temporal food tracking in Europe is probably a function of the greater representation of migratory birds.

Another difference between our findings and those from Europe was the influence of fruiting plant diversity on frugivore biomass. This phenomenon has not been reported from Europe, probably because in temperate systems there are few fruiting species. In the more diverse subtropical environment of our study, where there were up to 19 fruiting species per site, the effect of fruiting plant diversity on frugivore biomass was approximately equal to that of fruit biomass.

Table 4.1. Explanatory power of fruit. Values are the percentage of variation in each component that was explained by fruit. For each feeding guild, two models are presented: a model with fruit biomass as the sole covariate (left hand column) and a model with fruit biomass plus additional covariates (right hand column); see Table 4.2 for the identities of the additional covariates. Models with landscape fruit availability as the main covariate are presented for fruit nomads. The bottom row gives the percentage of total variation in frugivore biomass explained by each model. NA indicates that the model did not explain variation for that component.

Variation component	Combined frugivores		Generalists		Specialists		Fruit nomads		
	Fruit biomass only	Fruit biomass + additional covariates	Fruit biomass only	Fruit biomass + additional covariates	Fruit biomass only	Fruit biomass + additional covariates	Fruit biomass only	Landscape fruit availability only	Landscape fruit availability + additional covariates
Site	13.7	30.5	NA	2.3	54.8	59.1	70.2	NA	60.8
Locality	56	67.5	45.6	68.3	23.7	69.5	19.7	49.9	74.9
Vegetation type	67.9	88.2	74.1	91.3	21	78.5	48.9	57.1	81.1
Month (1-24)	10.3	NA	8.8	NA	9.5	NA	NA	NA	NA
Season	NA	NA	NA	NA	NA	NA	8.7	18.2	8.1
Year	21.6	34.8	22.7	18.4	25.3	51.2	26.2	6.8	53.1
Site × season	31.7	4.1	23.4	43.7	29.6	NA	NA	NA	NA
Locality ×	35.4	42.6	21.5	27.5	30	19.9	9.9	29.3	34.1

season								
Vegetation type × season	17.7	NA	16.9	10.6	43.7	38.4	63.0	17.5	56
Vegetation type × year	11.4	24.7	35.1	49.6	NA	11.1	23.9	28.4	63.2
Season × year	NA	-6.3	11.1	NA	NA	21.3	0.2	NA	NA
Residual	3.3	4.5	2.4	2.9	4.7	4.7	4.40	1.7	5
Total variation explained	20.2	26.3	16	21.4	9.8	17.8	7.8	8.4	15.8

Table 4.2. Probabilities of inclusion in model of additional candidate covariates. Probabilities above 0.75 (marked with an asterisk) indicate substantial evidence that the covariate should be included in the model. Values in brackets are model-averaged, standardized regression coefficients for covariates with substantial support. Fruit biomass is the main covariate in all models except that for fruit nomads; the main covariate for the fruit nomad model is landscape fruit availability.

	Number of species in fruit at a site	Total number of fruiting species at a site (summed over 2 years)	Landscape fruit availability (modelled within 5 grid cells [~ 1.275 km])	Fruit biomass measured on-site	Mean monthly temperature	Rainfall over previous 3 months	Above-ground plant biomass
Combined frugivores	0.98* [0.29 ± 0.10]	0.91* [0.30 ± 0.15]	0.60	-	0.31	0.38	0.44
Generalists	0.95* [0.23 ± 0.10]	0.94* [0.34 ± 0.17]	0.76* [0.16 ± 0.12]	-	0.28	0.29	0.27
Specialists	0.94* [0.20 ± 0.08]	0.25	0.23	-	0.30	0.43	0.99* [0.31 ± 0.11]
Fruit nomads	0.94* [0.12 ± 0.05]	1.0* [0.24 ± 0.04]	-	0.65	0.30	0.29	0.88* [0.12 ± 0.07]

Table 4.3. Strength of spatial and temporal fruit-tracking at the site-scale. Values

represent standardized linear slopes, as in Fig. 4.5.

	Spatial tracking: standardized linear slope among sites	Temporal tracking: mean standardized linear slope within sites.
Combined frugivores	1.5	0.5
Generalists	1.1	0.4
Specialists	1.1	0.4
Fruit nomads	0.5	0.2

Figure 4.1. Study region, showing locations of survey sites and extent of vegetation cover.

Figure 4.2. Partitioning of variation in frugivore and fruit biomass (explanation on following page).

Figure 4.2. Partitioning of variation in frugivore and fruit biomass. Boxplots show posterior distributions of finite-population standard deviations for each source of variation (i.e. variance components plotted as SDøs, which have the same scale as the log-transformed response variables); bars are posterior medians, boxes and dotted lines show 50% and 95% credibility intervals, respectively. The dark-shaded boxes show the amounts of variation within each component (residual variation is the largest source of variation, followed by vegetation type); the light-shaded boxes show residual variation in a model with fruit biomass as a predictor of bird biomass (i.e. variation in bird biomass not attributed to variation in fruit biomass). The difference between total (dark box) and residual (light box) variation indicates the amount of variation in each component that can be explained by fruit biomass. Where the dark box is far to the right of the light box (as for vegtype), fruit biomass explained a substantial proportion of the variation for that component. Where the dark box is to the left of the light box (as for season), fruit biomass did not explain variation. The dots in the ‑frugivore biomassøplot show the residual variation when additional covariates are included in the model (see Table 4.2 for the identities of the covariates); dots far to the left of the light grey boxes (as for ‑vegtypeø) indicate that the additional covariates substantially increased the explanatory power of the model.

Figure 4.3. Seasonal changes in the distribution of (a) fruit biomass and (b) frugivore biomass among vegetation types. Open circles = temperate rainforest; closed circles = weedy regrowth; open triangles = dry sclerophyll forest; open squares = subtropical rainforest; closed triangles = wet sclerophyll forest. In Camphor Laurel season (April to August) biomass of both fruit and frugivores was depressed in subtropical

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rainforest and elevated in weedy regrowth, suggesting that birds shifted from subtropical rainforest into weedy regrowth in response to changes in fruit availability.

Figure 4.4. Partitioning of variation in biomass of (a) generalist frugivores; (b) specialist frugivores; and (c) fruit nomads (the latter modelled as a function of landscape fruit availability). See Fig. 4.2 for detailed explanation.

Figure 4.5. Fruit tracking by combined frugivores at the site-scale separated into spatial (between sites) and temporal (between months at a site)

components (explanation on following page).

Figure 4.5. Fruit tracking by combined frugivores at the site-scale separated into spatial (between sites) and temporal (between months at a site) components. The left-hand panel shows the modelled relationship between mean fruit biomass and mean frugivore biomass for the 83 sites. The line of best fit (solid line) has slope 1.5 (Table 4.3); the dotted lines show the 95% credible interval. The right hand panel shows the modelled relationship between fruit anomaly (departure from the mean fruit biomass for a given site) and frugivore anomaly (departure from the mean value of frugivore biomass for a given site) for the 1 992 site-months; lines of best fit are shown for the 83 sites (mean slope = 0.50: Table 4.3). Note that the two panels have different scales.

Declaration for Thesis Chapter 5

In the case of Chapter 5, the nature and extent of my contribution to the work was as follows:

Nature of contribution	Extent of contribution (%)
I conceived the study, performed all of the fieldwork and 50% of the statistical analyses, and was the primary author of the manuscript.	80%

The following co-authors contributed to the work:

Name	Nature of contribution
Dr Ralph Mac Nally	Ralph Mac Nally contributed ideas to the work and co-authored the manuscript.
Dr James Thomson	James Thomson contributed ideas to the work, assisted with statistical analyses and helped write the –statistical analysesø section.

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidateøs and co-authorsø contributions to this work.

Candidateøs Signature		Date
Main Supervisorøs Signature		Date

Chapter 5 Regional-scale resource tracking by nectarivorous birds

Abstract

Aim. To document and explain regional patterns of nectarivorous bird biomass at multiple spatial and temporal scales.

Location. A 300 000 ha region in subtropical eastern Australia.

Methods. We counted birds and flowers at 83 sites monthly for 24 mo. We used Bayesian multi-level ANOVA to partition variance in nectarivore biomass into spatial (locality, site, vegetation type), temporal (month, season, year) and spatio-temporal components, and to examine the influence of potentially explanatory variables (flower abundance, vegetation structure and floristics, and modelled climate) on nectarivore biomass.

Results. Flower abundance explained much of the variation in nectarivore biomass; variables relating to climate and vegetation had little additional influence. Most variation was spatial: nectarivore biomass was greater in vegetation types and at sites with more flowers. Birds tracked seasonal changes in flowering among localities and vegetation types, but not to the extent warranted by variation in flower abundance. A lack of purely temporal variation in nectarivore biomass suggests that there were no major population fluctuations or net movements into or out of the study region. The strength of resource-tracking varied with the importance of nectar in the diet: specialist nectarivores tracked flowering quite closely, but tracking by generalists was weak.

Conclusions. Food availability was the greatest influence on bird biomass. Nectarivores tracked the spatial patterning of flowering and, to a lesser extent, its

spatio-temporal dynamics ó but, in the absence of large-scale migration, were unable

to respond to purely temporal changes in food availability.

Introduction

Resource availability is a key driver of the distribution and abundance of organisms. Bird abundance has often been explained in terms of the availability of foods such as insects (Lefebvre et al. 1994), nectar (Ford and Paton 1985, Cotton 2007) and fruit (Rey 1995, Moegenburg and Levey 2003). In a given region, food availability varies spatially (e.g. between habitat types, Blake and Loiselle 1991), temporally (e.g. between seasons: Ting et al. 2008) and spatio-temporally (e.g. where the distribution of food across habitat types changes seasonally, Haugaasen and Peres 2005).

Ecological theory predicts that such variations will be ‑tracked‑ by consumers, such that consumer abundance should always be proportional to food availability (Pulliam and Caraco 1984). Many studies have found evidence of some degree of resource tracking (e.g. Levey 1988, Rey 1995), although constraints such as travel costs and imperfect knowledge of food distribution mean that the perfect matching predicted by theory is rarely achieved in natural systems (Kennedy and Gray 1993). Patterns of food tracking exhibit considerable diversity: some species have been found to track food strongly, others weakly or not at all (Telleria et al. 2008, Blendinger et al. 2012). Even within a species, seasonal visitors may track food more closely than territorial residents (Telleria and Perez-Tris 2007). Several studies have noted that patterns of resource tracking are highly dependent on the scale of analysis (Burns 2004, Garcia and Ortiz-Pulido 2004). For example, Franklin and Noske (1999) found that Rainbow Lorikeets *Trichoglossus haematodus* in northern Australia tracked nectar at the scale of 0.5-ha quadrats, while Little Friarbirds *Philemon citreogularis* tracked nectar at much larger scales.

Nectar is an important food for birds, and many plants rely on birds for pollination: there are over 8 000 bird-pollinated species in the Americas alone (Nicolson and Fleming 2003). The mutualism between nectarivorous birds and nectar-producing plants has driven the radiation of three major avian families: the new world hummingbirds (Trochilidae), the sunbirds (Nectariniidae) of Africa and Asia, and the Australasian honeyeaters (Meliphagidae). Nectarivores are particularly prominent in Australia, where the honeyeaters are the largest avian family and birds from many other lineages also consume nectar. The dominant Australian nectar-producing plants are the eucalypts (the genera *Eucalyptus*, *Corymbia* and *Angophora* in the Myrtaceae). Although eucalypts may produce nectar in large quantities (Law and Chidel 2008), their flowering patterns are notoriously irregular (Law et al. 2000): most species flower unreliably, at intervals of several years (Birtchnell and Gibson 2006). Birds must cope with such an unpredictable food supply by resource tracking and/or diet switching, which involves eating alternative foods (such as insects, lerps, manna, honeydew and fruit) during periods of nectar shortage (Paton 1980). Species differ in their use of these strategies. At one extreme are ±blossom nomadsø (Keast 1967), highly mobile specialist nectarivores that track nectar over great distances ó sometimes > 1,000 km (Saunders and Heinsohn 2008). Conversely, diet switching allows the persistence of more or less sedentary generalists that eat nectar when available but survive for long periods without it (Franklin and Noske 1999). Other birds combine both strategies, diet switching to some extent and tracking nectar over relatively short distances.

Many studies (e.g. Ford and Paton 1985, McFarland 1986) have shown that nectarivorous bird abundance over small areas (< 20 km^2) increases and decreases in response to changes in nectar availability (i.e. that nectarivores track the temporal

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availability of nectar at small spatial scales). However, such studies can only speculate about where the 'additional' birds may have come from or gone to. A more complete understanding of resource-tracking requires studies over large areas. Because of the difficulties of measuring nectar, the few studies of food-tracking by nectarivores over large areas have used flowering as a proxy for nectar availability. McGoldrick and Mac Nally (1998) found that flowering by *Eucalyptus* spp. drove the abundance of nectarivorous birds over 1000s of km^2, but French et al. (2003) were unable to establish a relationship between nectarivorous bird numbers and the presence of *Eucalyptus* flowers (flower abundance was not measured). Hart et al. (2011) found weak positive relationships between flower density of *Metrosideros polymorpha* and the densities of three nectarivorous birds over an elevational gradient in Hawaii (a fourth species showed no relationship); their findings imply a degree of local resource-tracking, but not mass movements between elevations.

We examined flower tracking by birds at multiple spatial and temporal scales across a 300 000 ha region in subtropical eastern Australia. The study region provides habitat for many nectarivorous birds, including several rare and threatened species (e.g. little lorikeet *Glossopsitta pusilla*, swift parrot *Lathamus discolor* and regent honeyeater *Xanthomyza phrygia*: NSW Threatened Species Conservation Act 1995). We counted birds and flowers over 24 months at 83 sites, then partitioned variance in nectarivore biomass into spatial, temporal, and spatio-temporal components, and examined the influence of flower abundance on each component. We chose biomass as our measure of the 'amount' of nectarivores because we believe it provides a more accurate picture of the capacity of a site to support birds than does abundance (a 132 g little lorikeet is not equivalent to an 8 g scarlet honeyeater *Myzomela sanguinolenta*). We asked the following questions: (1) what are the spatial, temporal and spatio-

temporal patterns of nectarivore biomass?; (2) are these patterns driven by food availability (i.e. do nectarivores track flowering)?; and (3) do the patterns differ among feeding guilds (generalists, specialists and blossom nomads)? Although many studies of resource tracking have not considered the effects of other factors, food is unlikely to be the only variable influencing consumers (Herrera 1998); for example, weather and vegetation structure have also been shown to affect frugivore abundance (Boyle et al. 2010, Crampton et al. 2011). We therefore asked: (4) which other variables, if any, influence nectarivore biomass?

Methods

Study region

The 314 400 ha study region is centred on the Bellinger Valley on the mid north coast of New South Wales, Australia, at $152^o\,43øE$, $30^o\,28øS$ (Fig. 5.1). Elevations range from sea level in the east to c. 1 600 m a.s.l. There is a moist subtropical climate with hot, humid summers and warm, drier winters. Temperature maxima in the Bellinger Valley range from $30^o\,C$ (January) to $20^o\,C$ (July); minima range from to $18^o\,C$ (January) to $5^o\,C$ (July). Rainfall (1,704 mm annually at Coffs Harbour) is highest in summer and autumn (mean March rainfall is 234 mm) and lowest in winter and spring (mean September rainfall is 61 mm).

Vegetation

Native vegetation persists over 75% of the study region (Fig. 5.1), mainly as large connected blocks. The principal vegetation type in the study region is sclerophyll forest dominated by *Eucalyptus* spp., many of which are important sources of nectar for birds. Wet sclerophyll forests (in which the understorey is dominated by fleshy-fruited plants that produce little nectar) occupy 33% of the study region, and dry

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sclerophyll forests (in which the understorey is not dominated by fleshy-fruited plants) 23%. ‑Coastal sclerophyll vegetationø is native vegetation < 10 km from the coast in which plants that produce nectar in winter and spring are prominent (e.g. coast banksia *Banksia integrifolia* subsp. *integrifolia*, broad-leaved paperbark *Melaleuca quinquenervia*, swamp mahogany *Eucalyptus robusta*, forest red gum *E. tereticornis* and winter-flowering populations of blackbutt *E. pilularis*). There are few nectar-producing plants in subtropical or temperate rainforest (12% and 7% of the study region, respectively). ‑Weedy regrowthø (1% of the study region) occurs where rainforest has been cleared and subsequently abandoned, and may include nectar-producing species such as silky oak *Grevillea robusta* and flooded gum *E. grandis*. The remainder of the study region consists of pasture and farmland, which have little habitat value for nectarivores, and urban areas, which may include high densities of nectar-producing plants.

Site selection

We used ArcGIS 9.3 (ESRI) software and a survey gap analysis procedure (Ferrier et al. 2007) to select 54 sites that sampled the range of native vegetation types and environmental conditions; sites were circular plots of 30-m radius. We located another 18 sites in representative areas of rainforest (the GIS mapping used in site selection did not discriminate between rainforest types) and 11 sites in weedy regrowth, which at that stage had not been mapped. Apart from the weedy regrowth sites, all sites were located in pairs c. 400 m apart; the walk between paired sites allowed us to collect additional data on flowering phenology (results not reported).

Field program

BAH visited each site regularly (usually monthly, sometimes more than once per month) from December 2007 to the end of November 2009, making 1 654 site visits that sampled 1 500 out of a possible 1 992 site-month combinations (24 months × 83 sites). Groups of nearby sites were visited on the same day, but we randomized the order in which sites were visited in each group, and the order in which groups were visited in each month. During each 20-min site visit BAH conducted a 7-min bird survey, then spent 13 min counting flowers (and fruit: results reported in Chapter 2).

Counting flowers

For each species in flower during a site visit, we counted the number of plants in flower and estimated the average number of flowers (or inflorescences) per plant. Only species known to provide nectar for birds (Marchant and Higgins 1990, 1993, Higgins and Davies 1996, Higgins 1999, Higgins et al. 2001, Higgins and Peter 2002, Higgins et al. 2006) were included in flower counts. For plants that produced inflorescences (principally *Banksia*, *Grevillea, Melaleuca*, and *Xanthorrhoea* spp.), we calculated the number of flowers by multiplying the number of inflorescences by the mean number of flowers per inflorescence, sourced from published data (Supplementary Table S4). Flower counts were summed for all species in flower to give the total flower abundance for each site visit. Where a site was visited more than once in a month, we used the average flower abundance for that site-month in analysis. We also recorded the number of species in flower for each site-month combination, and calculated the total number of flowering species at each site and locality (summed over two years).

Counting birds

We conducted a 7-min point count of birds at the commencement of each site visit. Each time birds were seen or heard, we noted the species and number of individuals, and used a laser range-finder to estimate the distance of the birds from the centre of the site. At the end of each 7-min count, we recorded the total number of individuals of each species that had occurred on-site. For example, if there were two Lewin's honeyeaters *Meliphaga lewinii* at a site at the beginning of a count; if these birds left the site during the count; and if another Lewin's honeyeater came onto the site during the count, then the total number of Lewin's honeyeaters recorded at the site for that count was three. All bird counts commenced within 5 hr of sunrise. For each count, we recorded shade temperature and scored cloud cover, wind, rain and noise on a scale of 0-4 (low to high). Data from bird counts conducted in noisy conditions (65 surveys where noise was 3 or 4 as a result of strong winds or singing cicadas) were discarded from analysis. For each site visit, we calculated the biomass of each species as follows: biomass = total number of individuals recorded on-site during count $\times$ average mass of an individual of that species (based on data in Marchant and Higgins 1990, 1993, Higgins and Davies 1996, Higgins 1999, Higgins et al. 2001, Higgins and Peter 2002, Higgins et al. 2006). We summed the biomass of all nectarivorous species recorded during that site-visit to obtain the total nectarivore biomass. All bird counts were conducted by BAH.

Guild classifications

Birds were classified as nectarivores using published data (Marchant and Higgins 1990, 1993, Higgins and Davies 1996, Higgins 1999, Higgins et al. 2001, Higgins and Peter 2002, Higgins et al. 2006) and field observations; where nectar was judged a substantial part of a bird's diet, the species was classified a nectarivore (Supplementary Table S3). Nectarivores were assigned to feeding guilds (generalists,

specialists and blossom nomads) based on a combination of published material (Keast 1967, Higgins and Davies 1996, Higgins 1999, Higgins et al. 2001, Higgins and Peter 2002, Higgins et al. 2006) and our own observations during the study (Supplementary Table S3). Specialist nectarivores are species that rely heavily on nectar for food, while generalists are species that are less reliant on nectar. Blossom nomads are specialist nectarivores thought or known to travel widely in search of nectar.

Vegetation variables

Vegetation variables were measured between April and August 2010; there was little evident seasonal variation. Variables were measured within a circle of 15-m radius around the centre of each site, after checking that results obtained this way were consistent with results obtained from measuring the entire (30-m radius) site in a pilot study (results not reported). We assigned each site to a vegetation type, which took precedence over the mapped vegetation type if there was a conflict. Canopy height was measured at the centre of each site with a laser range-finder. Trees were counted, identified to species and classed as saplings (< 10 cm diameter at breast height [DBH]), small (10-25 cm DBH), small-medium (25-40 cm DBH), medium (40-60 cm DBH), large (60-80 cm DBH) or very large trees (>80 cm DBH). Exact DBHs were recorded for all trees with DBH $\times$ 40 cm. The numbers of liana (woody vine) stems, trees with basal hollows, trees with hollow-bearing limbs, stumps and dead trees were counted, and the volume and biomass of fallen logs calculated, using a mean density of 0.6 t m^{-3} for fallen timber (Mac Nally et al. 2002). Above-ground plant biomass estimates were derived using the general allometric equations for rainforest and eucalypt forest vegetation types given on page 70 of Keith et al. (2000). Five 2.5 m $\times$ 2.5 m quadrats were randomly located at each site, within which ground cover (percentage leaf litter, vegetation, rock and bare ground), percentage cover of

vegetation < 2 m, Leaf Area Index (measured using a CI-130 Digital Plant Canopy Imager: CID Bio-Science), and plant species richness were recorded.

Environmental variables

Monthly data on rainfall, temperature maxima and solar exposure at a 0.05^{o} grid scale for January 2007 to November 2009 were obtained from the Australian Water Availability Project (http://www.eoc.csiro.au/awap/, accessed 10/11/2010), and were used to derive rainfall totals for periods of 2, 3, 6, 9 and 12 months prior to a given month. Data for mean annual rainfall (0.025^{o} grid scale), mean monthly and annual evapotranspiration rates (0.1^{o} grid scale), mean monthly and annual numbers of frost days (0.05^{o} grid scale), annual temperature (mean, maximum and minimum: 0.025^{o} grid scale), mean and minimum monthly temperature (0.025^{o} grid scale), mean monthly and annual sunshine hours (0.025^{o} grid scale), and mean monthly and annual solar exposure (0.05^{o} grid scale) were obtained from the Australian Bureau of Meteorology on 15/10/2010. GIS layers (100-m grid scales) for wetness, annual temperature (mean, maximum and minimum), mean annual solar radiation, slope, moisture index, mean rainfall of driest quarter, mean annual rainfall, elevation and aspect were obtained from the NSW Department of Environment and Conservation. We used ArcGIS 9.3 (ESRI) to derive 100-m grid scale layers for ‒distance from coastø and ‒distance from nearest watercourseø Data for Gross Primary Productivity (GPP) at 0.0025^{o} grid scale were obtained from the Australian National University (Berry et al. 2007) on 15/06/2011 and used to derive GPP totals for periods of 2, 3, 6, 9 and 12 months prior to a given month.

Statistical analyses

We used Bayesian multi-level analysis of variance (ANOVA) (Gelman 2005, Qian and Shen 2007) to partition variation in flower abundance and nectarivore biomass into spatial and temporal components, and to examine the relationship between nectarivore biomass and flower abundance at multiple spatial and temporal scales. Bayesian multilevel ANOVA uses hierarchical regression models to partition variation in response variables among sources of variation. The basic model is:

$$y_i = \alpha + \sum_{s=1}^{S} \beta_{l_i}^s + \varepsilon_i$$

model (1)

In model (1), α is the grand mean, the βs are linear coefficients corresponding to group level effects (deviations from conditional means) within each of S sources of variation (factors), and ε_i is the residual error. $\beta_{l_i}^s$ is the coefficient for level l (e.g. sclerophyll forest) of factor s (e.g. vegetation type) relevant to datum i. The coefficients within each source s were drawn from exchangeable normal prior distributions, $\beta_l{}^s \sim Normal(0, \sigma_l s^{\uparrow}2$) with the corresponding standard deviations assigned uniform priors, $\sigma_s \sim Uniform(0, maxsd)$, where $maxsd$ was $\gg$ SD(y). The variance component for factor s is estimated by σ_s^2 (the ─supra-population∅ variance) or by the variance of the coefficients, var(β^s) (the ─finite-population∅ variance: Gelman 2005). We used the latter measure because it is more stable for factors with few sampled levels, and more relevant when all levels of interest have been sampled (e.g. vegetation type). The two measures are essentially equivalent for factors with many levels.

The spatial components in our models were site, locality and vegetation type (hereafter vegtype), and the temporal components were month [16́24], season, year and season × year (among-year variation in seasonal patterns). We also included four spatio-temporal terms: site × season, locality × season, vegtype × season, vegtype ×

year. Other interaction terms, including 3-way interactions, generally had near-zero variance components in initial model fitting, and were excluded from final models. Localities were groups of sites within a 2-km radius; we arrived at this distance after trialling various radii from 500 m to 5 km, and finding that 2 km was the smallest radius that resulted in clear differences between the effects of locality and site. 'Season' represented flowering seasons based on the main nectar-producing species at different times of year. The four seasons were: Blackbutt (November to January); Pink Bloodwood (February and March); Coast Banksia (April to September); and Silky Oak (October).

To examine the association between nectarivore biomass and flower abundance, we added spatial and temporal components of flowering as covariates to models of nectarivore biomass. The spatial flowering covariate was the mean flower abundance over 24 months at each site ($\overline{n_s}$). The temporal flowering covariate was the deviation from the site-specific mean in each survey ($n'_{sm} = n_{sm} - \overline{n_s}$). We assessed how much variation in nectarivore biomass was explained by flower abundance at each spatial and temporal scale by comparing the variance components in models with and without flowering covariates. We used Bayesian model selection, implemented with reversible jump MCMC (Lunn et al. 2009, Thomson et al. 2010), to assess the influence of a range of additional variables on nectarivore biomass. Bayesian model selection uses Bayes factors (ratios of marginal likelihoods) to weight model structures (combinations of variables), and yields model-averaged regression coefficients and posterior probabilities that each variable is a predictor (has non-zero coefficient: Wintle et al. 2003, Thomson et al. 2007). The set of additional candidate predictors was derived from expert knowledge and literature (Ferrier et al. 2002), and included climate, vegetation, and landscape contextual variables (Table 5.2).

Landscape nectar availability was estimated by using Boosted Regression Trees (Elith et al. 2008) to model nectar scores (derived from flower counts and unpublished data on floral visitation by birds) for each site-month as a function of vegetation type, calendar month and the environmental variables listed above, then mapping predicted nectar scores at a resolution of 0.0025°. We built the Boosted Regression Tree model using the gbm() package in R (R Core Team 2012) with default learning rate (0.001), bag.fraction (0.5), maximum interaction depth (5), and 10-fold cross-validation to determine the optimum number of trees. Landscape nectar availability for each month was the sum, for each grid cell in the study region, of the mapped values of predicted nectar score within 5 grid cells, excluding grid cells where vegetation type was mapped as cleared (where nectar availability was effectively zero) or urban (for which we lacked nectar availability data).

The full model relating nectarivore biomass to flower abundance and additional covariates was:

$$y_i = \alpha + \sum_{s=1}^{S} \beta_{l_i}^g + \beta_1^f . \overline{n_{s_i}} + \beta_2^f . n_{sm_i}^{\cdot} + \sum_{j=1}^{Q} \gamma_j x_{ij} + \varepsilon_i \qquad \text{model (2)}$$

In model (2), the β^fs are the linear coefficients associated with the spatial and temporal components of flowering, the γs are model-averaged linear coefficients associated with Q additional candidate covariates, and the remaining parameters are defined in model (1).

All models were estimated by Markov chain Monte Carlo with WinBUGS software (v. 14: Lunn et al. 2000) using the reversible jump add-on (Lunn et al. 2009) for model selection and spline fitting. Parameter posterior distributions were sampled over 3 independent chains of 50 000 iterations each, after 20 000 iteration burn-in periods (results discarded). Examination of chain histories and Brooks-Gelman-Rubin

diagnostics confirmed that adequate MCMC mixing and convergence were achieved. We used 'raw' measurements of bird counts, because attempting to account for detection error may produce biases at least as great as the biases that arise when detection eror is ignored (Welsh et al. 2013). Response variables and covariates with skewed distributions were log-transformed.

Results

Flowering

Approximately one quarter (28.8%) of the variation in flower abundance was partitioned into spatial components (site, locality and vegtype), 19.3% into spatio-temporal components (the site × season, locality × season, vegtype × season and vegtype × year interactions) and 3.4% into temporal components (month, season, year and the season × year interaction) (Fig. 5.2); 48.4% (the residual in Fig. 5.2) could not be allocated. Vegetation type (which accounted for 15.2% of the variation in flower abundance) was the largest single component, followed by site (12.8%) and the site × season (9.6%) and vegtype × season (7.5%) interactions (Fig. 5.2): there were more flowers in certain vegetation types (particularly coastal sclerophyll) and sites, and there were seasonal changes in the distribution of flowers across vegetation types and sites. In particular, there was a spike in flower abundance in coastal sclerophyll vegetation during Banksia season (April to September: Fig. 5.3a).

Nectarivores

Twenty species of nectarivorous birds were recorded on-site during surveys (Supplementary Table S3). Generalist nectarivores comprised 57% of the total nectarivore biomass, specialists 43%, and blossom nomads (a sub-guild of specialists) 36%. The species that contributed the most biomass were Lewin's honeyeater

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(43.3%), rainbow lorikeet (16.3%), silvereye *Zosterops lateralis* (5.7%), yellow-faced honeyeater *Lichenostomus chrysops* (5.5%), noisy friarbird *Philemon corniculatus* (5.0%), musk lorikeet *Glossopsitta concinna* (4.7%), and red wattlebird *Anthochaera carunculata* (4.6%). Nectarivores were present in 887 of the 1 435 site-months used in analysis, and every site had nectarivores during at least one month of the study.

Approximately one quarter (23.5%) of the variation in combined nectarivore biomass was partitioned into spatial components (site, locality and vegtype), 7.5% into spatio-temporal components (the site × season, locality × season, vegtype × season and vegtype × year interactions) and 3.4% into temporal components (month, season, year and the season × year interaction) (Fig. 5.2); 65.6% (the residual in Fig. 5.2) could not be allocated. Vegetation type (which accounted for 13.1% of the variation in biomass) was the largest single component, followed by site (8.7%) (Fig. 5.2); nectarivore biomass was greater at certain sites and in certain vegetation types (particularly coastal sclerophyll vegetation). The locality × season (3.2%) and vegtype × season (3.0%) interactions imply a degree of seasonal movement between localities and vegetation types: in particular, nectarivores appeared to move into coastal sclerophyll vegetation during Banksia season (April to September; Fig. 5.3b, c).

The distribution of nectarivore biomass differed between guilds. The pattern for generalist nectarivores (Fig. 5.4a) was similar to the overall pattern. Specialist nectarivores and blossom nomads exhibited greater spatio-temporal variation than other nectarivores (Fig. 5.4b and c): spatio-temporal components accounted for 13.0% and 14.4% of variation in biomass for specialist nectarivores and blossom nomads, respectively. Relatively strong vegtype × season interactions (which accounted for 7.7% and 8.7% of the variation in biomass for specialist nectarivores and blossom nomads, respectively) indicate substantial seasonal shifts between vegetation types. In

particular, biomass of specialist nectarivores and blossom nomads in coastal sclerophyll vegetation was depressed during Blackbutt season (November to January), and elevated during Pink Bloodwood and Banksia seasons (February-March and April-September, respectively: Fig. 5.3c).

The vegtype $\times$ year interaction (Fig. 5.4c) accounted for 4.4% of the variation in blossom nomad biomass, indicating that the distribution of blossom nomads across vegetation types differed between the two years of the study.

Nectar tracking

For combined nectarivores, flower abundance explained 14.8% of the variation in bird biomass (Table 5.1). In particular, flower abundance explained the preference of nectarivores for certain vegetation types and sites, as well as seasonal movements between localities (Fig. 5.2 and Table 5.1). The inclusion of extra covariates relating to climate and vegetation added little to the explanatory power of the model (Tables 5.1 and 5.2).

The nature of resource tracking differed among nectarivore guilds. Generalist nectarivores exhibited only weak tracking, whereas specialist nectarivores and blossom nomads tracked flowering quite strongly (Table 5.1); 2.9% of the variation in generalist biomass was explained by flower abundance, compared to 31.7% for specialists and 17.2% for blossom nomads (Table 5.1). Flowering largely explained seasonal movements between vegetation types, localities and sites for specialists and blossom nomads, but not for generalists (Table 5.1). To determine whether alternative resources, such as fruit, might be influencing the distributions of generalist nectarivores, we fitted the model for generalists with fruit biomass, which was measured on-site during surveys, as an additional candidate covariate; the probability of inclusion of fruit biomass in the model was 0.99. When fruit biomass was included

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as the main covariate, it explained 8.3% of the variation in generalist nectarivore biomass (cf. flower abundance, which explained only 2.9%: Table 5.1).

Besides flower abundance, generalist nectarivore biomass was positively associated with the number of flowering species at a site (summed over 2 yr) and mean monthly temperature (Table 5.2). Blossom nomad biomass was positively influenced by landscape nectar availability (modelled within 1.275 km), and negatively influenced by rainfall over the previous 6 months (Table 5.2). The addition of these extra covariates did not greatly increase the explanatory power of the models for generalists and blossom nomads (Table 5.1).

All guilds exhibited stronger spatial than temporal resource-tracking (Table 5.3): at the site-scale, the slope of the line of best fit for spatial tracking by combined nectarivores was 0.76, cf. 0.48 for temporal tracking (Fig. 5.3).

Discussion

Patterns of nectarivore biomass

Most of the variation in combined nectarivore biomass was spatial: biomass varied among vegetation types and sites (circles of 30-m radius), but less among localities (circles of 2-km radius). Spatio-temporal variation was also important: nectarivores moved seasonally between localities, vegetation types, and ó to a lesser extent ó sites, following the changing availability of flowers; this was particularly the case for specialists and blossom nomads. There was relatively little temporal variation in nectarivore biomass, suggesting that there were no major population fluctuations or mass movements into or out of the study region.

The lack of temporal variation in nectarivore biomass is perhaps surprising, considering that more than half of the species we recorded are known to make

migratory movements of some sort. Some species have resident populations in the study region that are augmented by winter migrants or birds on passage (e.g. yellow-faced honeyeater and silvereye); some have small resident populations that are outnumbered by summer migrants (e.g. spangled drongo *Dicrurus bracteatus* and olive-backed oriole *Oriolus sagittatus*); some make semi-regular seasonal movements within the study region and perhaps beyond (e.g. scarlet honeyeater, noisy friarbird and rainbow lorikeet); and some appear to track flowering at very large scales, possibly vacating the study region entirely (e.g. little lorikeet and musk lorikeet). The lack of temporal variation in nectarivore biomass might have resulted from complementary movements (e.g. of summer and winter migrants) into and out of the study region. Alternatively, the lack of temporal variation might indicate that most nectarivore movements were confined within the region. The latter explanation appears likely, given that flower abundance also varied relatively little over time, and that true long-distance migrants (i.e. species of which most or all birds are at times absent) comprised only a small proportion (<1%) of nectarivore biomass.

Differences between feeding guilds

Specialists and blossom nomads exhibited much greater spatio-temporal variation than generalists, moving seasonally among vegetation types, localities and sites. The greater mobility of specialists and blossom nomads is probably associated with a more restricted diet: whereas generalist biomass is relatively unaffected by spatio-temporal variation (perhaps because generalists mostly remain in one place, switching to other foods when nectar is scarce), specialists and blossom nomads follow the changing distribution of nectar across the landscape.

Blossom nomads differed from specialists in several ways. First, the distribution of blossom nomad biomass among vegetation types differed between

years. Whereas other guilds were seemingly constrained to a somewhat regular annual cycle, the movements of blossom nomads were relatively dynamic ó much like the flowering patterns of the eucalypts on which they feed (Law et al. 2000). Another difference was that blossom nomad biomass was positively influenced by landscape nectar availability (modelled within 1.275 km); this suggests that blossom nomads, many of which are highly gregarious, track flowering at relatively large scales.

Influences on nectarivore biomass

Flower abundance was an important influence on nectarivores, explaining from 2.9% (for generalists) to 31.7% (for specialists) of the variation in biomass (Table 5.1). These values are likely to be underestimates, because the biomass values for most site-month combinations were derived from only a single 7-minute bird count, and hence were highly susceptible to stochastic variability arising from the small-scale, short-term comings and goings of birds (the residuals in Figs 5.2 and 5.4).

Measuring nectar is the most accurate way of assessing the availability of food for nectarivores, but is difficult and time-consuming ó particularly where, as in the present study, much of the nectar resource is in the forest canopy. Because it was not feasible to measure nectar production over the large spatial and temporal extents of our study, we used flower abundance to estimate resource availability; this was also the approach adopted by previous studies of nectarivores at regional scales (MacNally and McGoldrick 1997, Hart et al. 2011). Given that the amount of nectar per flower varies between species, individuals and flowers of an individual (Law and Chidel 2007), flower abundance may not accurately reflect nectar availability; it is likely that nectarivores track food more strongly than our results for flower tracking suggest.

The inclusion of variables relating to climate and vegetation increased the explanatory power of models of nectarivore biomass by only a small amount (< 1%

for combined nectarivores: Table 5.1). This does not imply that biomass did not vary between vegetation types (it did, substantially) or along climatic gradients, merely that such variations were associated with, and probably caused by, variations in flower abundance.

Generalists exhibited only weak nectar tracking, partly because they were also influenced by the availability of other food types: fruit was a stronger influence on generalist biomass than was flower abundance. The explanation is that the majority of generalist biomass (76%) was contributed by Lewin's honeyeater, a species that feeds extensively on fruit (Higgins et al. 2001). Thus, patterns of flower tracking by generalists and combined nectarivores, among which generalists predominated, were probably obscured by birds tracking fruit. For example, the movement by combined nectarivores (and particularly generalists) into subtropical rainforest in Pink Bloodwood season (Fig. 5.3a, b) was most likely driven by fruit availability, which was high in subtropical rainforest in that season (unpublished data), rather than by flowering. Patterns of flower tracking were clearer among specialist nectarivores (i.e. species whose diets consist mostly of nectar) than among other guilds: flower abundance explained 31.7% of the variation in specialist biomass (cf. only 2.9% for generalists).

Effects of variation in detectability

Our results may have been affected to some degree by variation in detectability: birds may have been more detectable in certain vegetation types, at certain seasons, or in certain weather conditions. We did not attempt to account for detection error, because such attempts may produce biases at least as great as the biases that arise when detection error is ignored (Welsh et al. 2013). Several lines of reasoning suggest that the effect of variations in detectability is likely to have been minor compared with the

effect of genuine variations in biomass. First, when we modelled nectarivore abundance as a function of two important variables that affect detectability (background noise and percentage sunlight on canopy), the explanatory power of the model was low relative to models that incorporated food availability, vegetation, or ó to a lesser extent ó climate (Chapter 6, Table 6.1). Second, above-ground plant biomass (which might be expected to affect detectability, with birds being more difficult to detect in denser vegetation) had a low probability of inclusion in the models of nectarivore biomass (Table 5.2). Third, we found that bird abundance (for all birds, not just nectarivores) was greatest in the densest vegetation types (weedy regrowth, subtropical rainforest and wet sclerophyll forest: Chapter 6, Fig. 6.3) ó whereas, if detectability were the dominant influence on observed patterns of bird abundance, then abundance would be greatest in more open vegetation types (e.g. dry sclerophyll forest).

Flower tracking in space and time

Ecological theory predicts a perfect match between resources and consumers, such that spatio-temporal variation in the distribution of resources results in equivalent variation in consumer abundance (Pulliam and Caraco 1984). Contrary to this prediction, we found that nectarivores did not move around to the extent warranted by variation in flower abundance (Table 5.4, Fig. 5.5). One implication is that flower abundance must have often been non-limiting during our study. If birds were limited by flower abundance, a reduction in flowering would force them to travel or else starve; either outcome would result in spatial and temporal tracking of equal strength. However, if flower abundance was non-limiting, a reduction in flowering would not force any birds to travel or to starve; this would result in the observed pattern of stronger spatial than temporal resource tracking.

Why should flower abundance have been non-limiting? Fluctuating resources are thought to limit bird populations during periods of scarcity ('bottlenecks': Wiens 1977, 1989). Ecological bottlenecks may be regular seasonal phenomena or, in the case of resources that fluctuate supra-annually, they may occur at intervals of a decade or more (Wiens 1977, 1989). Nectar availability in Australia undergoes wide supra-annual variations related to rainfall (Law et al. 2000), and it is conceivable that bird biomass in our study region may have been limited by past bottlenecks. Rainfall was above average during the study (1 738-2 347 mm p.a. at Coffs Harbour, cf. the annual mean of 1 704 mm), but there had been below-average rainfall between 2000 and 2007 (1 090 mm in 2003 was the lowest annual total since 1968). Nectar would have been generally in over-supply during our study if nectarivore populations had been limited by, and had not yet recovered from, earlier periods of drought-induced shortage. An alternative possibility is that biotic interactions such as predation and parasitism may have prevented nectarivore populations from reaching carrying capacity (Andrewartha and Birch 1954).

Assuming that bird fitness increases as the ratio of resource availability to bird biomass increases (which seems likely: Shochat et al. 2002), then even where flower abundance is non-limiting, the observed pattern of stronger spatial than temporal tracking would develop only if there were constraints on the capacity of birds to travel. There are several reasons why birds might be reluctant or unable to move across the landscape. Travel is energetically costly; breeding birds cannot move far from the nest; some species are territorial; and movements outside of a well-known area are likely to result in decreased foraging efficiency and increased predation risk. Also, because birds lack perfect knowledge of resource distribution (Kennedy and

Gray 1993), there is no guarantee that travel will lead a bird to an area with more food.

Given that constraints on travel are likely to apply to many or even most birds, and that food availability is likely to limit consumer populations only occasionally, stronger spatial than temporal resource tracking may be the norm in closed systems (i.e. those without major influxes or effluxes of consumers). In such systems, the strength of temporal tracking should increase as resources become scarcer, or when constraints on movement are relaxed (e.g. outside the breeding season, or among non-breeding migrants). This is supported by Telleria and Perez-Trisøs (2007) finding that frugivorous birds in Spain exhibited stronger spatial than temporal tracking, but that temporal tracking was much stronger among over-wintering migrants than among resident birds.

Conclusion

We found that nectarivore biomass was governed by food availability, and that variables relating to climate and vegetation structure had little additional effect. Most variation in food availability and nectarivore biomass was spatial. Nectarivores also tracked changing patterns of food availability across the region, but not to the extent that might have been expected, given the degree of spatio-temporal variation in flower abundance; this suggests that nectar was generally non-limiting during the study. Temporal variation in nectarivore biomass (and flower abundance) was low, implying that most nectarivore movements were confined within the study region.

Table 5.1. Strength of flower tracking. Values are the percentage of variation in nectarivore biomass that was explained by flower abundance for each component. The summary (bottom two rows) gives the percentage of total variation explained by flower abundance alone, and by flower abundance plus the additional covariates listed in Table 5.2.

Component	Combined nectarivores	Generalist nectarivores	Specialist nectarivores	Blossom nomads
Site	39.8	10.1	90.6	15.7
Locality	NA	NA	NA	NA
Vegetation type	51.0	6.9	69.0	15.1
Month (1-24)	36.8	15.5	36.6	28.9
Season	10.8	22.6	23.4	29.2
Year	NA	35.0	9.1	11.7
Site × season	25.1	NA	71.4	30.0
Locality × season	49.4	13.8	80.1	77.8
Vegetation type × season	15.6	NA	65.9	67.1
Vegetation type × year	NA	28.5	0.7	4.4
Season × year	5.9	18.0	41.9	33.4
Residual	6.0	1.4	13.2	13.1
Total variance explained by	14.8	2.9	31.7	17.1

flower abundance				
Total variance				
explained by				
flower abundance	15.6	4.4	31.7	17.7
and additional				
covariates				

Table 5.2. Probabilities of inclusion in model of additional candidate covariates. Probabilities above 0.75 (marked with an asterisk) indicate substantial evidence that the covariate should be included in the model. Values in brackets are model-averaged, standardized regression coefficients for variables with substantial support.

	Total number of flowering species at a site (summed over 2 yr)	Modelled nectar availability within 5 grid cells (approx. 1.275 km)	Mean monthly temperature	Rainfall over previous 6 mo	Gross primary productivity over previous 3 mo	Above-ground plant biomass
Combined nectarivores	0.54	0.55	0.56	0.26	0.44	0.45
Generalists	0.70	0.31	0.82* (0.21 ± 0.17)	0.26	0.31	0.38
Specialists	0.56	0.53	0.36	0.64	0.35	0.31
Blossom nomads	0.27	0.92* (0.12 ± 0.06)	0.40	0.85* (-0.10 ± 0.06)	0.49	0.32

Table 5.3. Strength of spatial and temporal flower-tracking at the site-scale. Values represent standardized linear slopes, as in Fig. 5.5.

	Slope of line of best fit (spatial tracking)	Mean slope of line of best fit for each site (temporal tracking)
Combined nectarivores	0.76	0.48
Generalists	0.35	0.26
Specialists	0.86	0.43
Blossom nomads	0.24	0.21

Figure 5.1. Study region, showing survey sites and extent of vegetation cover.

Figure 5.2. Partitioning of variation in nectarivore biomass and flower abundance (explanation on following page).

Figure 5.2. Partitioning of variation in nectarivore biomass and flower abundance. Boxplots show posterior distributions of finite-population standard deviations for each source of variation (i.e. variance components plotted as SDs, which have the same scale as the log-transformed response variables); bars are posterior medians, boxes and dotted lines show 50% and 95% credibility intervals, respectively. The dark-shaded boxes show the amounts of variation within each component (*residual* and *vegtype* are the largest sources of variation); the light-shaded boxes show residual variation in a model with flower abundance as a predictor of bird biomass (i.e. variation in nectarivore biomass not attributed to variation in flower abundance). The difference between total (dark box) and residual (light box) variation indicates the amount of variation in each component that was explained by flowering. Where the dark box is to the right of the light box (as for *site*), flower abundance explained a substantial proportion of the variation for that component. Where the dark box is to the left of the light box (as for *locality*), flowering did not explain variation. The dots in the ‑nectarivore biomassø plot show the residual variation when additional covariates are included in the model (see Table 5.3 for the identities of the covariates).

Figure 5.3. Seasonal variation among vegetation types for (a) flower abundance; (b) combined nectarivores; and (c) specialist nectarivores. Open circle = coastal sclerophyll vegetation; closed circle = weedy regrowth; open triangle = dry sclerophyll forest; open square = subtropical rainforest; closed triangle = temperate rainforest; cross = wet sclerophyll forest. Seasons: Blackbutt: November to January;

PBW (Pink Bloodwood): February and March; Banksia: April to September; Silky Oak: October. Patterns for generalist nectarivores and blossom nomads (not shown) were similar to those for combined nectarivores and specialists, respectively.

Figure 5.4. Partitioning of variation in biomass of (a) generalist nectarivores; (b) specialist nectarivores; and (c) blossom nomads. Explanations as for Fig. 5.2

Figure 5.5. Flower tracking by combined nectarivores at the site-scale separated into spatial (between sites) and temporal (between months at a site) components (explanation on following page).

Figure 5.5. Flower tracking by combined nectarivores at the site-scale separated into spatial (between sites) and temporal (between months at a site) components. The left-hand panel shows the modelled relationship between mean flower abundance and mean nectarivore biomass for the 83 sites. The line of best fit has slope 0.76 (Table 5.3); the dotted lines show the 95% credible interval. The right hand panel shows the modelled relationship between flowering anomaly (departure from the mean flower abundance for a given site) and nectarivore anomaly (departure from the mean value of nectarivore biomass for a given site) for the 1 992 site-months; lines of best fit are shown for the 83 sites (mean slope = 0.48: Table 5.3). Note that the two panels have different scales.

Declaration for Thesis Chapter 6

In the case of Chapter 6, the nature and extent of my contribution to the work was as follows:

Nature of contribution	Extent of contribution (%)
I conceived the study, performed all of the fieldwork and 50% of the statistical analyses, and was the primary author of the manuscript.	80%

The following co-authors contributed to the work:

Name	Nature of contribution
Dr Ralph Mac Nally	Ralph Mac Nally contributed ideas to the work and co-authored the manuscript.
Dr James Thomson	James Thomson contributed ideas to the work, assisted with statistical analyses and helped write the 'statistical analyses' section.

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work.

Candidate's Signature		Date
Main Supervisor's Signature		Date

Chapter 6   What drives the abundance of forest birds? Effects of food availability, primary productivity and vegetation

Abstract

Aim. To document spatio-temporal patterns of forest bird abundance; and to compare the roles of food availability, primary productivity, and vegetation in explaining them.

Location. A 300 000 ha region in subtropical eastern Australia.

Methods. We counted birds and flowers and measured fruit biomass at 83 sites monthly for 24 mo. We used Bayesian multi-level ANOVA to partition variation in bird abundance into spatial (locality, site), temporal (month, season, year) and spatio-temporal components, and to examine the influence on abundance of variables relating to food availability, primary productivity (derived from climate models and satellite telemetry) and vegetation.

Results. Variation in bird abundance was mostly spatial; temporal variation (mostly as seasonal fluctuations) and spatio-temporal variation (mostly as seasonal movements between localities) were less marked. Food availability explained the most variation in bird abundance, followed by vegetation; the influence of primary productivity was relatively weak. Spatial variation in abundance was best explained by vegetation and food availability, temporal variation by productivity, and seasonal spatio-temporal variation by food availability and productivity.

Conclusions. Food availability was the most important influence on bird abundance, followed by vegetation type. Primary productivity had only a weak influence on

abundance, apparently because vegetation characteristics determined the proportion of

production available as food for birds.

Introduction

Understanding patterns of abundance is a central task in ecology. Recent interest in community-wide abundance has centred on its role in elucidating the positive relationship between species richness and primary productivity (Currie et al. 2004, Clarke and Gaston 2006). According to the ‗more individuals‗ hypothesis, there are more species in areas with greater productivity because these areas support more individuals (Wright 1983, Srivastava and Lawton 1998). Investigations of the ‗more individuals‗ hypothesis have found a positive relationship between community-wide bird abundance and productivity or associated climatic variables (water availability, temperature, actual evapo-transpiration etc.) at global and continental scales (Pautasso and Gaston 2005, Evans et al. 2006). The mechanisms underlying the productivity-abundance relationship have seldom been investigated, but productivity is thought to drive abundance through its effects on the availability of food and other resources (Wright 1983, Evans et al. 2006). Productivity is in turn influenced by vegetation characteristics (some habitats are more productive than others: Melillo et al. 1993), nutrient availability, and climate (Cramer et al. 1999).

At smaller scales, community-wide abundance has often been related to vegetation characteristics: numerous studies have found that population densities are affected by habitat type (e.g. Loyn 1985, Recher et al. 1991) and/or vegetation structure (Mills et al. 1991). Floristic and structural characteristics might affect populations directly, by providing shelter and facilitating thermoregulation (Carrascal et al. 2012), and/or indirectly, by influencing food availability, which is often unevenly distributed among habitat types (Blake and Loiselle 1991).

Food availability is a key driver of animal abundance, imposing an upper limit on population size (White 2008). Food availability has seldom been evaluated for an entire community, but at the level of species and feeding guilds it governs the densities of many taxa, including fish (Grenouillet et al. 2002), mammals (Heithaus and Dill 2002), reptiles (Diaz and Carrascal 1991) and birds (Rey 1995). Both primary productivity and vegetation characteristics operate at least partly through their effects on food, but few studies of community-wide abundance have attempted to measure food availability.

We sought to compare the influence of primary productivity, vegetation, and the availability of two important foods (fruit and flowers) on community-wide bird abundance across a 300 000 ha region in subtropical eastern Australia. Because food availability and productivity vary in time and space, we incorporated both spatial and temporal variation into the survey design. We counted birds, measured fruit and counted flowers monthly over 24 months at 83 sites, then partitioned variation in bird abundance into spatial, temporal, and spatio-temporal components and examined the influence of explanatory factors on each component. We asked: (1) what are the spatio-temporal patterns of forest bird abundance?; and (2) how well do productivity, vegetation and food availability explain these patterns?

Methods

Study region

The 314 432 ha study region is centred on the Bellinger Valley on the mid north coast of New South Wales, Australia, at $152^o 43\o E$, $30^o 28\o S$ (Fig. 6.1). Elevations range from sea level in the east to c. 1 600 m a.s.l. There is a moist subtropical climate with hot, humid summers and warm, drier winters. Temperature maxima in the Bellinger

Valley range from 30° C (January) to 20° C (July); minima range from to 18° C (January) to 5° C (July). Rainfall (1,704 mm annually at Coffs Harbour) is highest in summer and autumn (mean March rainfall is 234 mm) and lowest in winter and spring (mean September rainfall is 61 mm).

Vegetation

Native vegetation persists over 75% of the study region (Fig. 6.1), mainly as large connected blocks. The principal vegetation type in the study region is sclerophyll forest dominated by *Eucalyptus* spp.. Wet sclerophyll forests (in which the understorey is dominated by soft-leaved plants) occupy 33% of the study region, and dry sclerophyll forests (in which soft-leaved plants are absent or uncommon) 23%. Subtropical rainforest (12% of the study region) has a complex structure and high diversity of trees; temperate rainforest (7% of the study region) has fewer vines, lianas and epiphytes, and lower tree diversity. 'Weedy regrowth' (1% of the study region) occurs where rainforest has been cleared and the land has later been abandoned; it often includes high densities of exotic species such as camphor laurel *Cinnamomum camphora*. The remainder of the study region consists of pasture, farmland and urban areas.

Site selection

We used ArcGIS 9.3 (ESRI) software and a survey gap analysis procedure (Ferrier et al. 2007) to select 54 sites that sampled the range of native vegetation types and environmental conditions; sites were circular plots of 30-m radius. We located another 18 sites in representative areas of rainforest (the GIS mapping used in site selection did not discriminate between rainforest types) and 11 sites in weedy regrowth, which at that stage had not been mapped. Apart from the weedy regrowth sites, all sites were

located in pairs c. 400 m apart; the walk between paired sites allowed the collection of additional data on flowering and fruiting phenology (results not reported).

Field program

BAH visited each site regularly (usually monthly) from December 2007 to the end of November 2009, sampling 1 500 out of a possible 1 992 site-month combinations (24 months × 83 sites). Groups of nearby sites were visited on the same day, but to reduce systematic biases we randomized the order in which sites were visited in each group, and the order in which groups were visited in each month. During each 20-min site visit, BAH conducted a 7-min bird survey, then spent 13 min counting flowers and fruit, and recording detections of additional bird species (results not reported).

Measuring fruit

For each species in fruit during a site visit, we counted the number of plants fruiting and estimated the average number of full-sized fruits per plant. Only fruits known to be eaten by birds were included in calculations of fruit biomass. For species whose full-sized fruits change colour as they ripen, we classed fruit as either ripe or unripe. Fruit biomass for each fruiting species was calculated by multiplying the number of plants in fruit by the average number of fruits per plant by the average wet fruit mass; the latter data were obtained by weighing × 20 fruits of each species in the field using a handheld spring balance. Fruit biomass was summed for all fruiting species to give the total fruit biomass for each site visit. Unripe camphor laurel fruits, which were seldom eaten in relation to their abundance, were excluded from measurements of fruit biomass. Where a site was visited more than once in a month, we used the average fruit biomass for that site-month in analysis. We also recorded the number of

species in fruit for each site-month, and calculated the total number of fruiting species at each site and locality (summed over two years).

Counting flowers

For each species in flower during a site visit, we counted the number of plants in flower and estimated the average number of flowers (or inflorescences) per plant. Only species known to provide nectar for birds (Marchant and Higgins 1990, 1993, Higgins and Davies 1996, Higgins 1999, Higgins et al. 2001, Higgins and Peter 2002, Higgins et al. 2006) were included in flower counts. For plants that produced inflorescences (principally *Banksia*, *Grevillea, Melaleuca*, and *Xanthorrhoea* spp.), we calculated the number of flowers by multiplying the number of inflorescences by the mean number of flowers per inflorescence, sourced from published data (Supplementary Table S4). Flower counts were summed for all species in flower to give the total flower abundance for each site visit. Where a site was visited more than once in a month, we used the average flower abundance for that site-month in analysis.

Counting birds

We (BAH undertook all surveys) conducted a 7-min point count of birds at the commencement of each site visit. Each time birds were seen or heard, we noted the species and number of individuals, and used a laser range-finder to estimate the distance of the birds from the centre of the site. At the end of each 7-min count, we recorded the total number of individuals of each bird species that had occurred on-site. For example, if there were two Lewin's honeyeaters *Meliphaga lewinii* at a site at the beginning of a count; if these birds left the site during the count; and if another Lewin's honeyeater came onto the site during the count, then the total number of

Lewin's honeyeaters recorded at the site for that count was three. All bird counts commenced within five hours after sunrise. For each count we recorded shade temperature, estimated the percentage of the canopy in sunlight, and scored cloud cover, wind, rain and noise on a scale of 0-4 (low to high). Data from bird counts conducted in noisy conditions (65 surveys where noise was 3 or 4 as a result of strong winds or singing cicadas) were discarded from analysis.

Guild classifications

Birds were classified as nectarivores, frugivores and insectivores using published data (Marchant and Higgins 1990, 1993, Higgins and Davies 1996, Higgins 1999, Higgins et al. 2001, Higgins and Peter 2002, Higgins et al. 2006) and field observations (Supplementary Table S3); where nectar, fruit or invertebrates were judged a substantial part of a species' diet, the species was assigned to the relevant guild. Guilds were not mutually exclusive, meaning that some species were members of more than one feeding guild. Apart from nectarivores, frugivores and insectivores, other feeding guilds made a negligible contribution to avian abundances.

Vegetation variables

Vegetation variables were measured between April and August 2010; there was little evident seasonal variation. Variables were measured within a circle of 15-m radius around the centre of each site, after checking that results obtained this way were consistent with results obtained from measuring the entire (30-m radius) site in a pilot study (results not reported). We assigned each site to a vegetation type, which took precedence over the mapped vegetation type if there was a conflict. Canopy height was measured at the centre of each site with a laser range-finder. Trees were counted, identified to species and classed as saplings (< 10 cm diameter at breast height

[DBH]), small (10-25 cm DBH), small-medium (25-40 cm DBH), medium (40-60 cm DBH), large (60-80 cm DBH) or very large trees (>80 cm DBH). Exact DBHs were recorded for all trees with DBH $\times$ 40 cm. The numbers of liana (woody vine) stems, trees with basal hollows, trees with hollow-bearing limbs, stumps and dead trees were counted. The volume and biomass of fallen logs was calculated using a mean density of 0.6 t m^{-3} for fallen timber (Mac Nally et al. 2002). Above-ground plant biomass estimates were derived using the general allometric equations for rainforest and eucalypt forest vegetation types given on page 70 of Keith et al. (2000). Five 2.5 m $\times$ 2.5 m quadrats were randomly located at each site, within which ground cover (percentage leaf litter, vegetation, rock and bare ground), percentage cover of vegetation < 2 m, Leaf Area Index (measured using a CI-130 Digital Plant Canopy Imager: CID Bio-Science), and plant species richness were recorded.

Environmental variables

Monthly data on rainfall, temperature maxima and solar exposure at a 0.05^{o} grid scale for January 2007 to November 2009 were obtained from the Australian Water Availability Project (http://www.eoc.csiro.au/awap/, accessed 10/11/2010), and were used to derive rainfall totals for periods of 2, 3, 6, 9 and 12 months prior to a given month. Data for mean annual rainfall (0.025^{o} grid scale), mean monthly and annual evapotranspiration rates (0.1^{o} grid scale), mean monthly and annual numbers of frost days (0.05^{o} grid scale), annual temperature (mean, maximum and minimum: 0.025^{o} grid scale), mean and minimum monthly temperature (0.025^{o} grid scale), mean monthly and annual sunshine hours (0.025^{o} grid scale), and mean monthly and annual solar exposure (0.05^{o} grid scale) were obtained from the Australian Bureau of Meteorology on 15/10/2010. GIS layers (100-m grid scales) for wetness, annual temperature (mean, maximum and minimum), mean annual solar radiation, slope,

moisture index, mean rainfall of driest quarter, mean annual rainfall, elevation and aspect were obtained from the NSW Department of Environment and Conservation. We used ArcGIS 9.3 (ESRI) to derive 100-m grid scale layers for 'distance from coast' and 'distance from nearest watercourse'. Data for Gross Primary Productivity (GPP) at 0.0025° grid scale were obtained from the Australian National University (Berry et al. 2007) on 15/06/2011 and used to derive GPP totals for periods of 2, 3, 6, 9 and 12 months prior to a given month.

Statistical analyses

We used Bayesian multi-level analysis of variance (ANOVA) (Gelman 2005, Qian and Shen 2007) to partition variation in resource availability and bird abundance into spatial and temporal components, and to examine the relationships between bird abundance and variables relating to food availability, primary productivity and vegetation at multiple spatial and temporal scales. Bayesian multilevel ANOVA uses hierarchical regression models to partition variation in response variables among sources of variation. The basic model may be expressed as:

$$y_i = \alpha + \sum_{s=1}^{S} \beta_{l_i}^s + \varepsilon_i$$

model (1)

In model (1), α is the grand mean, the β's are linear coefficients corresponding to group level effects (deviations from conditional means) within each of *S* sources of variation (factors), and ε_i is the residual error. $\beta_{l_i}^s$ is the coefficient for level *l* (e.g. sclerophyll forest) of factor *s* (e.g. vegetation type) relevant to datum *i*. The coefficients within each source *s* were drawn from exchangeable normal prior distributions, $\beta_l{}^s \sim Normal(0, \sigma_l s^2)$) with the corresponding standard deviations assigned flat uniform priors, $\sigma_s \sim Uniform(0, maxsd)$, where *maxsd* was >> SD(*y*). The variance component for factor *s* is estimated by σ_s^2 (the 'supra-population' variance)

or by the variance of the coefficients, var(β^s) (the 'finite-population' variance: Gelman 2005). We used the latter measure because it is more stable for factors with few sampled levels, and more relevant when all levels of interest have been sampled (e.g. vegetation type). The two measures are essentially equivalent for factors with many levels.

We used model (1) to partition variation in abundance into spatial and temporal components at multiple scales. The spatial components in our models were site and locality, and the temporal components were month [1-24], season and year. We also included two spatio-temporal terms: site × season and locality × season. Other interaction terms, including 3-way interactions, generally had near-zero variance components in initial model fitting, and were excluded from final models. Localities were groups of sites within a 2-km radius; we arrived at this distance after trialling various radii from 500 m to 5 km, and finding that 2 km was the smallest radius that resulted in clear differences between the effects of locality and site. =Seasonø represented seasons based on the mean rainfall and temperature of the calendar months. The four seasons were: December-January; February-March; April to August; and September to November.

Having quantified variation in bird abundances using model (1), we incorporated a range of covariates to determine how much variation, at each spatial and temporal scale, could be explained by different environmental factors. The general model was:

$$y_i = \alpha + \sum_{s=1}^{S} \beta_{l_i}^s + \sum_{j=1}^{Q} \gamma_j x_{ij} + \varepsilon_i$$

model (2)

In model (2), the γøs are linear coefficients associated with Q candidate predictors, and the remaining parameters are as defined in model (1). With the βøs now

conditional on covariate effects, the resulting variance components partition the residual variation in abundance (i.e. variation not explained by covariates).

We modelled total abundances of all birds and abundances of each guild (frugivores, nectarivores and insectivores). For each response variable, we fitted four covariate models to explore the explanatory power of ‑food availabilityø, ‑vegetationø, and ‑productivityø variables separately and in combination. The ‑food availabilityø model included flower abundance and fruit biomass as predictors for all response variables, and, for frugivore abundance only, the number of plant species in fruit and total number of fruiting plant species summed over 24 months. The ‑vegetationø model included canopy height and vegetation type, the ‑productivityø model included monthly GPP, monthly mean temperature and rainfall of previous 3 months (climate variables may strongly influence productivity), and the ‑combinedø model included all the above predictors. All models also included ‑percentage of canopy in sunlightø and ‑noiseø to account for possible variability in bird detectability among surveys. We also fitted a ‑detectabilityø covariate model which included ‑percentage of canopy in sunlightø and ‑noiseø

We used Bayesian model selection, implemented with reversible jump MCMC (Lunn et al. 2009, Thomson et al. 2010), to assess the influence of individual covariates on each response variable. Bayesian model selection uses Bayes factors (ratios of marginal likelihoods) to weight model structures (combinations of variables), and yields model-averaged regression coefficients and posterior probabilities that each variable is a predictor (has non-zero coefficient: Wintle et al. 2003, Thomson et al. 2007). We also used piecewise linear regression splines to test for non-linear associations between bird abundance and covariates, by replacing the β^føs and γøs in (2) with free-knot linear splines (Thomson et al. 2010). We found no

substantial evidence of non-linear effects, and therefore report results for linear models only.

All models were estimated by Markov chain Monte Carlo with WinBUGS software (v. 14: Lunn et al. 2000) using the reversible jump add-on (Lunn et al. 2009) for model selection and spline fitting. Parameter posterior distributions were sampled over 3 independent chains of 50000 iterations each, after 20 000 iteration burn in periods. Examination of chain histories and BGR diagnostics confirmed that adequate MCMC mixing and convergence were achieved. We used ₋raw₀ measurements of bird counts, because attempting to account for detection error may produce biases at least as great as the biases that arise when detection eror is ignored (Welsh et al. 2013). Response variables and covariates with skewed distributions were log-transformed.

Results

We recorded 13 567 birds of 105 species in the 1 500 site-month combinations surveyed; mean abundance was 8.3 birds per site-month. Insectivores comprised 96% of the individuals counted (of which 23% were also frugivores and/or nectarivores), frugivores 21% and nectarivores 22%. Fruit and/or nectar were important dietary items for c. 32% of the individuals counted.

Approximately one-quarter (26.1%) of the variation in bird abundance was partitioned into spatial components (site and locality), 6.0% into spatio-temporal components (the site × season and locality × season interactions) and 4.5% into temporal components (month, season and year) (Fig. 6.2); 63.8% (the residual in Fig. 6.2) could not be partitioned. Locality (which accounted for 13.5% of the variation in abundance) and site (12.4%) were the largest components. The locality × season interaction (5.4%) suggests that birds moved seasonally among localities (Fig. 6.2).

Combined covariate models explained from 17ó27% of the variation in bird abundance (Table 6.1). For all birds combined, for frugivores and for nectarivores, food availability explained the most variation in abundance (Table 6.1). Vegetation explained the most variation in insectivore abundance, and also explained substantial amounts of variation in the abundance of all birds combined and of frugivores. Productivity explained relatively little variation in bird abundance (Table 6.1).

Flower abundance, fruit biomass and vegetation type were the variables most often and most strongly supported for inclusion in models, along with two detectability variables (noise and percentage of canopy in sunlight: Table 6.2). The relationships between bird abundance and flower abundance, fruit biomass, vegetation type and primary productivity are shown in Fig. 6.3. There was substantial evidence for the inclusion of monthly mean temperature in the ÷combinedø and ÷productivityø covariate models of nectarivore abundance (Table 6.2). The probabilities of inclusion for productivity variables (GPP, monthly mean temperature, and rainfall of previous 3 mo) were greater in the ÷productivityø covariate models, which excluded vegetation and food variables, than in the ÷combinedø models (Table 2), suggesting that productivity is correlated with food availability and/or vegetation.

Spatial variation in bird abundance was best explained by food and vegetation; seasonal spatio-temporal variation was best explained by food and productivity; and temporal variation was best explained by productivity (for all birds combined and for insectivores; temporal variation in frugivore and nectarivore abundance was not well explained) (Table 6.3).

Discussion

Food availability and vegetation explained the most variation in bird abundance: there were more birds where there was more food (fruit and flowers), and more birds in some vegetation types than others. It is difficult to distinguish between the effects of food and vegetation, because fruit and flower availability were correlated with vegetation type (Chapter 4, Fig. 4.2, and Chapter 5, Fig. 5.2). However, in all but the models for insectivores (the guild whose main food was not measured), food availability explained more variation than vegetation, suggesting that food was the single most influential factor affecting abundances. It might be argued that some of the variation in abundance between vegetation types could have been caused by variation in detectability, with birds being more difficult to detect in taller and/or denser vegetation. However, bird abundance was greatest in the taller, denser vegetation types (weedy regrowth, subtropical rainforest and wet sclerophyll forest: Fig. 6.3), and canopy height was not supported for inclusion in models of bird abundance (Table 6.2), suggesting that detection error caused by dense and/or tall vegetation was not a major influence on the patterns we observed.

Fruit and nectar were important dietary items for only 32% of the individuals counted, but food explained more variation in total bird abundance than did vegetation or productivity. Fruit and flower availability also explained substantial amounts of variation in insectivore abundance. This might be due partly to the overlap between feeding guilds (fruit and nectar were important dietary items for 23% of the insectivores counted), and partly because flowers and fruit attract insects.

Variables relating to productivity were relatively unimportant in models that included food and vegetation, but were more influential when food and vegetation were excluded, suggesting that productivity may have influenced bird abundance through its effects on food and vegetation. In particular, productivity was an important

influence on temporal variation in abundance (Table 6.3), probably because recruitment of juveniles and migratory influxes were timed to coincide with periods of high productivity. Compared with food and vegetation, however, the influence of productivity on bird abundance was relatively weak.

Given that productivity *must* set an upper limit on abundance, why was its influence not more evident? There was limited spatial variation in productivity in our study, but substantial spatial variation in abundance (coefficient of variation among sites was 0.04 for GPP, cf. 0.40 for abundance), suggesting that the *proportion* of production consumed by birds varied spatially. For example, although productivity was similar among vegetation types (mean productivity in the most productive vegetation type was only 1.06 times that in the least), vegetation type had a powerful effect on bird abundance; this implies that a greater proportion of production was available as food for birds in some vegetation types (weedy regrowth, subtropical rainforest and wet sclerophyll forest) than in others. Meehan et al. (2004) found that the proportion of production consumed by birds varied spatially, although not necessarily among vegetation types. The notion that differing proportions of primary production are available to birds in different vegetation types is not strongly supported by the handful of studies that have examined bird-community energetics in northern hemisphere deciduous and coniferous forests (e.g. Holmes and Sturges 1975, Alatalo 1978), but is untested for rainforests or eucalypt forests, the main vegetation types in our study region.

The low explanatory power of productivity might be a result of a mismatch in measurement grain: our data on bird abundance were derived from ~ 0.28 ha sites, whereas productivity was measured over ~ 6.5 ha GIS cells. However, similar disparities in grain have not prevented previous studies from detecting stronger

productivity-abundance relationships than we did (Evans et al. 2006, Monkkonen et al. 2006). Another possibility is that our productivity model, which was derived from satellite measurements of NDVI (normalised difference vegetation index), may have been inaccurate. At the upper range of values, such as in the dense vegetation that characterizes much of our study region, sensor saturation limits the ability of NDVI to detect differences in photosynthetic activity (Phillips et al. 2008). However, previous studies using NDVI have found relatively strong relationships between productivity and bird abundance or species richness (Hurlbert 2004, Evans et al. 2005), including in areas of dense forest (Ding et al. 2006). Although site-based productivity data would be preferable to broad-scale values derived from NDVI, it appears unlikely that the weak productivity-abundance relationships we observed were merely the effect of a mismatch between grains or of deficient productivity measurements.

Our models explained only a small proportion of the variation in bird abundance. We attribute this partly to our survey methodology: the abundance value for most site-month combinations was obtained from only a single 7-minute bird count, meaning that measurements were vulnerable to stochastic variability arising from the small-scale, short-term comings and goings of birds; this is reflected in the large residual components in the models. When examining only spatial variation (which, with a mean 19 surveys per site and 39 per locality, was relatively immune from stochasticity) the models explained much greater proportions of the variation in bird abundance (Table 6.3). However, even when only spatial variation was considered, between 25.3% (for frugivores) and 57.2% (for insectivores) of the variation in abundance could not be explained by the models. What might account for the unexplained variation? Studies in eucalypt forests, the dominant vegetation type in our study region, have shown that foliar nutrients such as nitrogen, potassium,

phosphorus and magnesium influence the abundance and/or species richness of arboreal marsupials (Braithwaite 1983, Cork and Catling 1996), arthropods (White 1993, Recher et al. 1996) and birds (Braithwaite et al. 1989, Recher et al. 1996). It is possible that foliar nutrient levels, which are related to soil characteristics, might account for much of the unexplained variation in bird abundance, probably through their effects on the biomass of folivorous arthropods. Nutrient levels might also partly explain the relationship between abundance and vegetation type, which appears to follow a fertility gradient: weedy regrowth, subtropical rainforest and wet sclerophyll forest ó the vegetation types where birds were most abundant ó occur on more fertile soils (e.g. on basalt or along creeks), whereas dry sclerophyll forest occurs on granitic soils and upper slopes. However, fertility is unlikely to account for the low abundance of birds in temperate rainforest, which occurs on a variety of soil types.

Most previous studies of productivity and bird abundance found a stronger relationship than we did, with productivity variables such as actual evapo-transpiration (Monkkonen et al. 2006, Symonds and Johnson 2008), temperature (Evans et al. 2006, Evans et al. 2008), NDVI (Hurlbert 2004), net primary productivity (Meehan et al. 2004, Ding et al. 2005) and rainfall seasonality (Williams and Middleton 2008) explaining between 15-71% of the variation in bird numbers (cf. 1.9-13.9% in our study). With few exceptions, these studies were at continental or global scales comprehending substantial variation in productivity. In the only study at a scale smaller than ours (Ding et al. 2005), the annual productivity of the poorest site was 0.33 that of the richest (cf. 0.75 for our study) due to the presence of a steep elevational gradient. Thus, the weak productivity-abundance relationship we observed may have been partly due to the low spatial variation in productivity across our study region.

Much of the recent interest in patterns of community-wide abundance has centred on its role in explaining the positive relationship between species richness and measures of environmental energy, such as primary productivity (Currie et al. 2004, Meehan et al. 2004, Evans et al. 2006). To the extent that we found that productivity had a positive effect on abundance, our results support the ‑more individualsø hypothesis, which posits that productive areas support more individuals. We did not seek to test the second part of the hypothesis (that areas with more individuals support more species), which has been investigated elsewhere (e.g. Pautasso and Gaston 2005, Evans et al. 2006). Notwithstanding its importance to species-energy theory, we consider that community-wide abundance is a matter of interest in its own right, with potentially far-reaching applications. For example, locating conservation reserves in areas of high abundance might conserve more biodiversity than locating equivalent reserves in low abundance areas.

Our study is a step towards developing a more comprehensive understanding of community-wide abundance. We investigated some of its main determinants, but took no account of potentially important factors such as interspecific interactions (Maron et al. in press) and landscape characteristics. We found that primary productivity was a distal driver of abundance, but that its effect was mediated by vegetation characteristics, which appeared to determine the proportion of productivity available as food for birds. Food availability was the strongest influence on bird abundance, followed by vegetation type, with productivity a distant third.

Table 6.1. Explanatory power of covariate models ('combined', 'food', 'vegetation', 'productivity' and 'detectability') of bird abundance, for all birds and for three feeding guilds; values are the percentage of variation explained.

Covariate model	All birds	Frugivores	Nectarivores	Insectivores
Combined	18.5	26.5	15.6	15.9
Food	11.1	21.7	16.2	8.3
Vegetation	10.0	17.6	0.5	10.0
Productivity	3.8	2.6	1.9	4.9
Detectability	2.4	0.6	0.7	3.2

Table 6.2. Probabilities of inclusion of variables in covariate models. Probabilities above 0.75 (bold type) indicate substantial evidence that the variable should be included in the model. Values in brackets are model-averaged, standardized regression coefficients for variables with substantial support.

Covariate model		Variable										
		Food				Productivity			Vegetation		Detectability	
		Flower abundance	Fruit biomass	Number of spp. in fruit	Total number of fruiting spp.	Monthly GPP	Monthly mean temperature	Rainfall of previous 3 months	Canopy height	Vegetation type	% canopy in sun	Noise (1-4)
All birds	Combined	1.00 (0.15 ± 0.02)	1.00 (0.11 ± 0.02)	-	-	0.33	0.09	0.08	0.51	1.00	0.98 (0.07 ± 0.02)	1.00 (-0.15 ± 0.02)
	Food	1.00 (0.13 ± 0.02)	1.00 (0.12 ± 0.02)	-	-	-	-	-	-	-	1.00 (0.07 ± 0.02)	1.00 (- 0.15 ± 0.02)
	Vegetation	-	-	-	-	-	-	-	0.09	0.98	0.99 (0.07 ± 0.02)	1.00 (-0.14 ± 0.02)

Covariate model		Variable										
		Food				Productivity			Vegetation		Detectability	
		Flower abundance	Fruit biomass	Number of spp. in fruit	Total number of fruiting spp.	Monthly GPP	Monthly mean temperature	Rainfall of previous 3 months	Canopy height	Vegetation type	% canopy in sun	Noise (1-4)
	Productivity	-	-	-	-	0.67	0.42	0.22	-	-	**1.00 (0.07 ± 0.02)**	**1.00 (-0.14 ± 0.02)**
	Detectability	**-**	**-**	-	**-**	-	-	-	-	**-**	**0.99 (0.07 ± 0.02)**	**1.00 (-0.14 ± 0.02)**
Frugivores	Combined	**0.93 (0.06 ± 0.02)**	**1.00 (0.17 ± 0.04)**	0.32	0.53	0.25	0.32	0.15	0.12	**1.00**	0.32	0.68
	Food	**0.90 (0.05 ± 0.02)**	**1.00 (0.16 ± 0.04)**	0.52	**0.94 (0.08 ± 0.04)**	-	-	-	-	-	0.56	**0.81 (0.03 ± 0.02)**
	Vegetation	-	-	-	-	-	-	-	0.06	**1.00**	0.11	0.39

Covariate model		Variable										
		Food				Productivity			Vegetation		Detectability	
		Flower abundance	Fruit biomass	Number of spp. in fruit	Total number of fruiting spp.	Monthly GPP	Monthly mean temperature	Rainfall of previous 3 months	Canopy height	Vegetation type	% canopy in sun	Noise (1-4)
	Productivity	-	-	-	-	0.47	0.74	0.33	-	-	0.58	**0.80 (0.03 ± 0.02)**
	Detectability	-	-	-	-	-	-	-	-	-	0.56	**0.78 (0.03 ± 0.02)**
Nectarivores	Combined	**1.00 (0.24 ± 0.02)**	**0.95 (0.07 ± 0.03)**	-	-	0.21	**0.94 (0.11 ± 0.05)**	0.24	0.10	0.63	0.42	0.41
	Food	**1.00 (0.24 ± 0.02)**	**0.99 (0.08 ± 0.02)**	-	-	-	-	-	-	-	0.61	0.55
	Vegetation	-	-	-	-	-	-	-	0.17	0.69	0.68	0.44
	Productivity	-	-	-	-	0.37	**0.94 (0.10 ± 0.06)**	0.36	-	-	**0.87 (-0.04 ±**	0.69

Covariate model		Variable										
		Food				Productivity			Vegetation		Detectability	
		Flower abundance	Fruit biomass	Number of spp. in fruit	Total number of fruiting spp.	Monthly GPP	Monthly mean temperature	Rainfall of previous 3 months	Canopy height	Vegetation type	% canopy in sun	Noise (1-4)
											0.02)	
	Detectability	-	-	-	-	-	-	-	-	-	0.85 (-0.03 ± 0.02)	0.70
Insectivores	Combined	1.00 (0.14 ± 0.02)	0.98 (0.08 ± 0.03)	-	-	0.25	0.09	0.09	0.55	1.00	0.95 (0.06 ± 0.02)	1.00 (-0.14 ± 0.02)
	Food	1.00 (0.13 ± 0.02)	1.00 (0.09 ± 0.02)	-	-	-	-	-	-	-	0.98 (0.06 ± 0.02)	1.00 (-0.14 ± 0.02)
	Vegetation	-	-	-	-	-	-	-	0.12	0.99	0.95 (0.06 ± 0.02)	1.00 (-0.14 ± 0.02)

Covariate model	Variable										
	Food				Productivity			Vegetation		Detectability	
	Flower abundance	Fruit biomass	Number of spp. in fruit	Total number of fruiting spp.	Monthly GPP	Monthly mean temperature	Rainfall of previous 3 months	Canopy height	Vegetation type	% canopy in sun	Noise (1-4)
Productivity	-	-	-	-	0.60	0.36	0.22	-	-	0.99 (0.06 ± 0.02)	1.00 (-0.14 ± 0.02)
Detectability	-	-	-	-	-	-	-	-	-	0.99 (0.06 ± 0.02)	1.00 (-0.14 ± 0.02)

Table 6.3. Amount of spatial, seasonal spatio-temporal, and temporal variation in bird abundance explained by covariate models, for all birds and for three feeding guilds. Values are the percentage of variation explained; NA indicates that the covariate model did not explain variation for that component.

		Spatial variation	Seasonal spatio-temporal variation	Temporal variation	Residual variation
All birds	Combined	49.8	29.6	NA	NA
	Food	21.9	26.0	NA	NA
	Vegetation	25.9	10.5	11.7	NA
	Productivity	NA	20.3	26.9	NA
	Detectability	NA	8.1	9.8	NA
Frugivores	Combined	74.8	15.4	NA	NA
	Food	58.4	17.3	NA	NA
	Vegetation	56.3	NA	2.0	NA
	Productivity	7.3	1.7	NA	NA
	Detectability	1.0	0.9	1.5	NA
Nectarivores	Combined	52.7	36.3	NA	NA
	Food	42.0	35.1	16.1	NA
	Vegetation	1.0	NA	NA	NA
	Productivity	12.8	NA	NA	NA
	Detectability	0.2	NA	5.3	NA
Insectivores	Combined	43.5	26.6	NA	NA
	Food	14.3	18.8	NA	NA
	Vegetation	26.7	9.8	19.7	NA
	Productivity	0.2	18.6	37.7	NA
	Detectability	NA	8.4	21.6	NA

Figure 6.1. Study region, showing survey sites and extent of vegetation cover.

Abundance (all birds)

Figure 6.2. Partitioning of variation in bird abundance (all birds). Boxes show

posterior distributions of finite-population standard deviations (Gelman 2005) for

each source of variation (i.e. variance components plotted as SDs, which have the

same scale as the log-transformed bird counts); bars are posterior medians, boxes and

dotted lines show 50% and 95% credible intervals, respectively. The dark grey boxes

show the amount of variation attributed to each component (apart from the residual

component, the greatest variation is among sites and localities). The light grey boxes

show residual variation in the combined covariate model. The difference between

total (dark box) and residual (light box) variation indicates the amount of variation in

each component that was explained by the combined covariate model (Table 6.3).

Where the dark box is to the right of the light box (as for locality), the model

explained a substantial proportion of the variation for that component. Where the dark

box is to the left of the light box (as for year), the model did not explain variation.

Figure 6.3. Plots of partial residuals of bird abundance modelled as a function of (a) mean flower abundance; (b) mean fruit biomass; and (c) mean GPP. Plot (d) shows differences in bird abundance among vegetation types; dots show means, bars show standard errors. WR = weedy regrowth; SRF = subtropical rainforest; ; WSF = wet sclerophyll forest; DSF = dry sclerophyll forest; TRF = temperate rainforest.

Chapter 7   General Discussion

I documented patterns of regional bird abundance and explained them in terms of food availability, vegetation and primary productivity. Most variation in bird abundance was spatial: there were more birds in certain vegetation types and where mean food availability was higher. Bird abundance also exhibited a degree of spatio-temporal variation, which was associated with seasonal changes in food availability and primary productivity: birds tracked the changing availability of fruit, flowers and plant production across the study region. Temporal variation, which was less marked than spatial and spatio-temporal variation, was chiefly associated with primary productivity, probably because influxes of migratory insectivorous birds and recruitment of juveniles occurred during times of high productivity.

Food (fruit and flower) availability was the dominant influence on bird abundance. Because food availability differed among vegetation types, the association between vegetation and bird abundance was also strong. Although variables relating to climate and primary productivity were important influences on food availability, they had only weak effects on bird abundance.

Patterns of fruit and nectar availability

Regional fruit availability followed a consistent annual cycle in the two years of study, with a peak from February to April and a ‗lean season‘ from July to November. I have not presented results for spatio-temporal variation in fruit biomass, but patterns were consistent between years: fruit biomass was high in subtropical rainforest from December to March (due to reliable fruiting by species such as giant pepper vine *Piper novaehollandiae* and bangalow palm *Archontophoenix cunninghamiana*), and in

weedy regrowth from February to August (due to reliable fruiting by species such as camphor laurel *Cinnamomum camphora*, large-leaved privet *Ligustrum lucidum* and white cedar *Melia azedarach*: unpublished data). Fruit (in varying quantities) was available in subtropical rainforest throughout the year, mainly due to asynchronously fruiting figs such as the giant strangler-fig *Ficus watkinsiana*.

The annual cycle of fruit availability in the study region was similar to those reported by previous studies in subtropical Australian rainforests (Holmes 1987, Innis 1989, Church 1997), suggesting that a single pattern prevails over a north-south distance of at least 500 km. The slight differences between my results and those of previous studies may relate to the methods used: I measured fruit biomass in all major vegetation types, whereas previous studies measured the number of species fruiting and were restricted to rainforests.

Temporal and spatio-temporal patterns of regional nectar availability in bushland differed between years, mostly due to irregular flowering by a few species of eucalypts. The one consistent feature of the annual nectar cycle was a period of scarcity in late winter and spring (August-September); this has also been identified as a time of scarcity in northern New South Wales by Law *et al*. (2000), and in eastern Australia generally by Eby and Law (2008). Reliable species (i.e. those that flower every year) were responsible for some consistent spatio-temporal patterns: in both years nectar availability was high in coastal areas between April and September (due to flowering by coastal species such as coast banksia *Banksia integrifolia* subsp. *integrifolia*, broad-leaved paperbark *Melaleuca quinquenervia*, swamp mahogany *Eucalyptus robusta* and forest red gum *E. tereticornis*), and moderately high at elevations above 600 m between February and May (due to flowering by montane *Banksia* spp.). Unlike fruit, which was always available somewhere in the region,

regional nectar availability at times was close to zero. Earlier studies of community-wide nectar production in Australia have reported similar severe nectar shortages over relatively small areas (< 20 km^2) (e.g. Pyke 1983, Pyke 1985, Collins and Newland 1986, McFarland 1986, Brady 2009); my study demonstrates that nectar scarcity may be much more widespread. Previous studies have used vegetation mapping to depict spatio-temporal patterns of regional nectar availability over large areas ($> 10\ 000$ km^2) in a 'typical' year (Woinarski et al. 2000, Eby and Law 2008); my study is among the first to measure and map 'actual' nectar availability (flowering) across a region, highlighting the importance of inter-annual variability and its implications for nectarivores.

Influences on fruit and nectar availability

The most influential variables in Boosted Regression Tree models of fruit and nectar availability were those relating to vegetation type, primary productivity and rainfall. Vegetation type (relative influence 17%), gross primary productivity (GPP) of the previous six months (15%) and GPP of the previous twelve months (9%) had the most influence on fruit biomass; this accords with earlier findings that primary productivity was the main environmental determinant of global fruit production (Ting et al. 2008, Hanya and Aiba 2010). Nectar availability in the study region was related most closely to GPP of the previous twelve months (relative influence 19%) and rainfall of the previous six months (7%). The development of remotely sensed measurements of primary productivity is relatively recent, and I am not aware of any previous attempts to examine the effect of productivity on flowering or nectar production at regional or greater scales. Previous studies have found that community-wide flowering patterns were affected by irradiance, temperature, heat sum (i.e. accumulated time above a

certain temperature) and rainfall (Smith-Ramirez and Armesto 1994, Wright and Schaik 1994, Diekmann 1996, Fenner 1998, Law et al. 2000, Birtchnell and Gibson 2006); these factors are all related to primary productivity (Cramer et al. 1999). Periods of fruit and nectar scarcity in the study region were associated with low rainfall over the previous six months (for nectar) and low productivity over the previous six months (for fruit).

Important plant species and habitats for frugivores and nectarivores

Assuming that consumer abundance is limited by lean-season food availability, then vegetation types and plant species that reliably provide nectar or fruit during periods of scarcity are likely to be crucial in sustaining nectarivore or frugivore populations. Weedy regrowth dominated by camphor laurel was the vegetation type in which fruit biomass was highest during the July-November lean season (unpublished data): total on-site fruit production by camphor laurel in these months was 194 kg, cf. the total on-site lean-season production of 576 kg. Coastal vegetation with coast banksia, swamp mahogany and forest red gum, and gardens with *Grevillea* cultivars, were the chief sources of nectar during the August-September lean season. Flowering patterns in gardens appeared to complement those in natural vegetation: peak nectar production in gardens (which occurred from August to October associated with a spike in flowering by *Grevillea* cultivars) coincided with a decline in nectar availability in bushland, raising the possibility that some nectarivores may move from bushland into gardens during these months. Although the value of garden plants as food sources for nectarivores is widely known (Catterall 2004), I am not aware that any previous studies have identified complementary flowering patterns between garden plantings and natural vegetation.

Mistletoes and garden *Grevillea* cultivars were the only groups of plants that provided nectar throughout the year, and the giant strangler-fig was the only species that provided a year-round source of fruit (unpublished data). These species may play important roles in sustaining bird populations. *Ficus* spp. are recognized as key foods for animals in many parts of the world (Janzen 1979, Kinnaird et al. 1996, Bleher et al. 2003, Westcott et al. 2005). Similarly, several previous studies have identified mistletoes as valuable nectar sources, both in Australia and globally (Ford et al. 1979, Turner 1991, Watson 2001).

Selecting native replacements for the camphor laurel

Camphor laurel, the most prolific source of lean-season food for frugivores in the study region, is an invasive weed that is the subject of control programs (Scanlon and the Camphor Laurel Taskforce 2000). Camphor laurel control could lead to declines in native frugivore populations unless offset by plantings of ‒equivalentø native species (Date et al. 1991, Date et al. 1996). I drew on earlier work identifying keystone fruiting species (Peres 2000, Westcott et al. 2005) and native equivalents to exotic fruiting plants (Gosper and Vivian-Smith 2006, Gosper and Vivian-Smith 2009) to develop a conceptual framework for prioritizing species to plant as replacements for camphor laurels. I propose that the best replacements for camphor laurels are species that: fruit reliably every year; fruit in the same months as the camphor laurel; are native; are easy to cultivate; and are preferred by important frugivores such as the topknot pigeon *Lopholaimus antarcticus* (a long-distance seed disperser) and threatened wompoo and rose-crowned fruit-doves (*Ptilinopus magnificus* and *P. regina*, respectively). The plants that scored highest for these criteria were various large figs *Ficus* spp., the common acronychia *Acronychia*

oblongifolia and saffronheart *Halfordia kendack*. Other useful species to plant for frugivore conservation include beach acronychia *A. imperforata*, native tamarind *Diploglottis cunninghamii* and bangalow palm *Archontophoenix cunninghamiana*.

Patterns of bird abundance and biomass

Abundance of all guilds combined

Although patterns of bird abundance are known to vary temporally and spatio-temporally (i.e. where the spatial pattern changes over time) (Blake and Loiselle 1991, Haugaasen and Peres 2007), few studies have sought to investigate the relative importance of spatial, temporal and spatio-temporal variation in regional bird abundance. Spatial components accounted for 26.1% of the total variation in bird abundance, and 71.5% of the variation that could be partitioned by models; birds were more abundant in certain vegetation types (weedy regrowth, subtropical rainforest and wet sclerophyll forest) and where mean food availability was higher. Spatio-temporal variation (16.4% of the variation that could be partitioned by models) was associated with seasonal changes in food availability and primary productivity; birds tracked the changing availability of fruit, flowers and plant production (which may have affected insect abundance) across the study region. Temporal variation in bird abundance (12.3% of the variation that could be partitioned) was chiefly associated with primary productivity, probably because influxes of migratory insectivorous birds and recruitment of juveniles occurred during times of high productivity.

Intra-regional movements such as those inferred here are often ignored in the species distribution mapping that underlies much conservation planning (e.g. Ferrier et al. 2002, Williams 2006), meaning that reserves may fail to protect the full extent of the habitat that an individual relies on over a year or lifetime. My finding that

regional bird abundance is subject to substantial spatio-temporal variation indicates that seasonal changes in bird distributions need to considered in conservation planning.

Biomass of frugivores and nectarivores

Most of the variation in frugivore and nectarivore biomass was spatial. Spatial variation accounted for 30.5% of the variation in frugivore biomass, or 79% of the variation that could be partitioned by models, and 23.5% of the variation in nectarivore biomass, or 68% of the variation that could be partitioned by models (all percentages in the remainder of this section are percentages of the variation that could be partitioned by models). Vegetation type was the single largest variance component for both guilds, accounting for 47% of variation for frugivores, and 38% for nectarivores; frugivore biomass was greatest in weedy regrowth and subtropical rainforest, nectarivore biomass in coastal sclerophyll forest. Variation between sites (circular plots of 30-m radius) was greater for nectarivores (25%) than frugivores (14%), whereas variation between localities (circles of 2-km radius) was greater for frugivores (18%) than nectarivores (4%). These results imply that nectarivores have a tendency to ʻzero inʼon small patches of suitable habitat, whereas frugivores are distributed more diffusely. This difference might be a result of energetic considerations, such that nectarivores need to spend more time feeding than frugivores, or of the territorial, resource-defence behaviour that has often been noted among nectarivorous birds (Mac Nally and Timewell 2005), but is less common in frugivores (Male 2002).

Spatio-temporal variation was greater for nectarivores (22%) than for frugivores (14%). Both guilds made seasonal movements between vegetation types, accounting for 9% of the variation in nectarivore biomass and 7% of the variation in

frugivore biomass. Nectarivores shifted into coastal sclerophyll vegetation between April and August, when coastal species such as coast banksia, broad-leaved paperbark and swamp mahogany were flowering; during the same months frugivores moved out of subtropical rainforest and into weedy regrowth, probably in response to fruiting by camphor laurels. Seasonal movements between localities were more important for nectarivores (9%) than for frugivores (4%). The greater spatio-temporal variation evident in nectarivores, compared with frugivores, may relate to differences in the patterns of fruit and nectar availability. Spatial patterns of fruit availability were largely consistent between years, and there were certain areas and vegetation types where fruit was available (in varying quantities) year-round. Nectar availability was less regular, and (apart from gardens) no part of the study region provided prolific nectar throughout the year. These patterns might have favoured the development of relatively sedentary life histories among frugivores, and relatively mobile life histories among nectarivores.

Compared with spatial and spatio-temporal variation, temporal variation in biomass was relatively low for both frugivores (7%) and nectarivores (10%). This suggests that there were no major population fluctuations or net movements into or out of the study region. The low temporal variation is perhaps surprising, considering that more than half of the nectarivorous species recorded (and also three species of frugivore) are known to make long-distance movements, at least in some parts of their ranges. Notwithstanding the capacity of many species to travel long distances, my findings suggest that most movements by frugivorous and nectarivorous birds were confined to the study region. The relatively low temporal variation in nectarivore and frugivore biomass reflected the patterns of food availability; temporal variation in fruit biomass accounted for only 10% of the variation that could be partitioned (cf.

54% for spatial variation), and temporal variation in flower abundance accounted for only 7% of variation (cf. 56% for spatial variation).

Patterns of variation in frugivore and nectarivore biomass differed among sub-guilds classified according to diet and known movement behaviour. 'Blossom nomads' and 'fruit nomads' exhibited greater spatio-temporal variation than other guilds, moving seasonally between vegetation types, localities and sites; spatio-temporal variation accounted for 47% of the variation in fruit nomad biomass, and 42% for blossom nomads. These movements were influenced by landscape food availability (modelled fruit or nectar within a radius of c. 1.3 km), suggesting that fruit and blossom nomads tracked food at larger scales than other guilds. Patterns in the variation of the biomass of specialists (i.e. species that eat mainly fruit or nectar) were different for frugivores and nectarivores. Spatio-temporal components accounted for only 9% of the variation in specialist frugivore biomass, but 32% of the variation in specialist nectarivore biomass; I interpret this as evidence that specialist frugivores were more sedentary than specialist nectarivores. The explanation for the greater mobility of specialist nectarivores may be that nectar availability is more variable and unpredictable than fruit availability.

Food tracking by frugivorous and nectarivorous birds

Given that spatio-temporal patterns of food availability may differ among years (Fredriksson 2006), that some birds track food over long distances (Holbrook et al. 2002, Saunders and Heinsohn 2008), and that the patterns observed are dependent on the scale of analysis (Burns 2004, Garcia and Ortiz-Pulido 2004), studies of avian food tracking ideally should examine multiple scales, for at least two years, over the largest area possible. There have been few multi-year, multi-scale studies of food

tracking at regional or greater scales (Telleria and Perez-Tris 2007, Guitian and Munilla 2008, Telleria et al. 2008); fewer still have sought to present a complete account of food tracking by sampling the full range of environmental variation in the region of interest. My study, which sampled all major combinations of vegetation types and climatic conditions, provides perhaps the most comprehensive account yet of regional food tracking by birds.

Food availability was an important influence on the biomass of both frugivores and nectarivores. Fruit biomass explained between 8.4% (for fruit nomads) and 20.2% (for all frugivores combined) of the variation in frugivore biomass, and flower abundance explained between 2.9% (for generalists) and 31.7% (for specialists) of the variation in nectarivore biomass. Flower abundance explained little variation in generalist nectarivore biomass because this guild was dominated by Lewin's honeyeater *Meliphaga lewinii*, a species that feeds extensively on fruit (Higgins et al. 2001); fruit availability explained more of the variation in generalist nectarivore biomass (8.3%) than did flower abundance. The values given above are likely to be underestimates, because the biomass value for most site-month combinations was obtained from only a single 7-minute bird count; the data were therefore vulnerable to stochastic variability, which may have accounted for the large residual components in the models (65.6% for nectarivores and 61.6% for frugivores). With few exceptions, the explanatory power of the models relating bird biomass to food availability did not increase, or increased very little, when climate and vegetation variables were added. This does not mean that biomass was not influenced by climate or vegetation, but that the influence of climate or vegetation on bird biomass was associated with, and probably caused by, variations in food availability.

Food availability strongly influenced spatial variation in nectarivore and frugivore biomass: biomass of both guilds was higher in sites and vegetation types with higher mean food availability. Food availability explained up to 90.6% (for specialists) of the variation in nectarivore biomass between sites, and up to 74.1% (for generalists) of the variation in frugivore biomass between vegetation types. Food availability was also an important influence on spatio-temporal variation in nectarivore and frugivore biomass: both guilds made seasonal movements between sites, localities and vegetation types in response to changes in the spatial distribution of food. Food availability explained up to 80.1% (for specialists) of seasonal movements between localities by nectarivores, and up to 43.7% (for specialists) of seasonal movements between vegetation types by frugivores. Food availability was less influential on temporal variation in frugivore and nectarivore biomass; flower abundance explained some of the variation in nectarivore biomass between months (up to 36.8%, for all guilds combined) and seasons (up to 29.2%, for blossom nomads), and fruit biomass explained up to 25.3% (for specialists) of the variation in frugivore biomass between years.

There were several differences between frugivores and nectarivores. Food-plant diversity was an important influence on the biomass of frugivores, but not of nectarivores. Frugivore biomass was greater at sites where there were more plant species in fruit (regression coefficient was 0.29 ± 0.10), and at sites with more fruiting plant species, summed over two years (regression coefficient was 0.30 ± 0.15). These preferences may have arisen because frugivores benefit from dietary variety (Herrera 1985) and because sites with higher fruiting plant diversity provide fruit for a greater portion of the annual cycle, minimising the need to travel. Because nectar consists only of sugar and water (unlike fruit, which also contains lipids and protein), feeding

on a diversity of plant species might be of less dietary benefit to nectarivores than to frugivores.

Ecological theory predicts a perfect match between resources and consumers, such that spatio-temporal variation in the distribution of resources results in equivalent variation in consumer abundance (Pulliam and Caraco 1984). Contrary to this prediction, I found that frugivores and nectarivores did not move around to the extent that might have been expected, given the degree of spatio-temporal variation in fruit availability: spatio-temporal components accounted for 37% of the variation in fruit and flower availability, but only 22% of the variation in nectarivore biomass and 14% of the variation in frugivore biomass. Both frugivores and nectarivores exhibited stronger spatial than temporal food tracking: at the site-scale, the slope of the line of best fit for spatial food tracking by frugivores was 1.5 (cf. 0.5 for temporal food tracking), and the slope of the line of best fit for spatial food tracking by nectarivores was 0.76 (cf. 0.5 for temporal tracking).

One implication of these results is that food abundance must have often been non-limiting during the study. If birds were limited by food abundance, a reduction in flower or fruit availability would force them to travel or else starve; either outcome would result in spatial and temporal tracking of equal strength. However, if food abundance were non-limiting, a reduction in flower or fruit availability would not force birds to travel or to starve; this would result in the observed pattern of stronger spatial than temporal resource tracking. Fluctuating resources are thought to limit bird populations during periods of scarcity ('bottlenecks': Wiens 1977, 1989). Ecological bottlenecks may be regular seasonal phenomena or, in the case of resources that fluctuate supra-annually, they may occur at intervals of a decade or more (Wiens 1977, 1989). Nectar and fruit availability may undergo large supra-annual variations

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related to rainfall (Law et al. 2000, Fredriksson 2006), and it is conceivable that bird biomass in the study region may have been limited by past bottlenecks. Rainfall was above average during the study (1 738 - 2 347 mm p.a. at Coffs Harbour, cf. the annual mean of 1 704 mm), but there had been below-average rainfall between 2000 and 2007 (1 090 mm in 2003 was the lowest annual total since 1968). Fruit and nectar would have been generally in over-supply during the study if frugivore and nectarivore populations had been limited by, and had not yet recovered from, earlier periods of drought-induced food shortage. Alternatively, biotic interactions such as predation and parasitism may have prevented the bird populations in the region from reaching carrying capacity (Andrewartha and Birch 1954), though there is no evidence for or against this hypothesis.

Assuming that bird fitness increases as the ratio of resource availability to bird biomass increases (which seems likely: Shochat et al. 2002), then even if food abundance were non-limiting, the observed pattern of stronger spatial than temporal tracking would develop only if there were constraints on the capacity of birds to travel. There are several reasons why birds might be reluctant or unable to move across the landscape. Travel is energetically costly; breeding birds cannot move far from the nest; some species are territorial; and movements outside of a well-known area are likely to result in decreased foraging efficiency and increased predation risk. Also, given that birds lack perfect knowledge of resource distribution (Kennedy and Gray 1993), there is no guarantee that travel will lead a bird to an area with more food.

Given that many species are likely to experience constraints on travel, and that food availability does not always limit consumer populations, stronger spatial than temporal resource tracking is probably the norm in closed systems (i.e. those without

major fluxes of consumers). In such systems, the strength of temporal tracking should increase as resources become scarcer, or when constraints on movement are relaxed (e.g. outside the breeding season, or among non-breeding migrants). This is supported by Telleria and Perez-Trisøs (2007) finding that frugivorous birds in Spain exhibited stronger spatial than temporal tracking, but that temporal tracking was much stronger among over-wintering migrants than among resident birds.

The few previous multi-year, multi-scale studies of regional food tracking have investigated fruit-frugivore systems in temperate Europe (Telleria and Perez-Tris 2007, Guitian and Munilla 2008, Telleria et al. 2008); my study is among the first in the tropical or subtropical regions where most nectarivores and frugivores birds live. Some important differences between my findings and those from Europe can be attributed to the greater proportion of long-distance migrants in European bird communities. Studies in Europe found that bird numbers tracked temporal changes in food availability, at least to some extent (Guitian and Munilla 2008, Telleria et al. 2008), whereas temporal tracking was very weak in my study region. Similarly, the only European study to have compared spatial and temporal tracking at the site-scale found that, in habitats dominated by over-wintering migrants, temporal tracking was almost as strong as spatial tracking (Telleria and Perez-Tris 2007) (the slope of temporal tracking was 83% of the slope of spatial tracking, cf. 33% in this study). Long-distance migrants are the dominant frugivores in many European systems, but comprised < 1% of the biomass of frugivores and nectarivores in the study region. Migratory birds are less constrained in their ability to travel than residents, allowing them to track spatio-temporal changes in food availability more closely. Thus, the greater degree of temporal and spatio-temporal food tracking in Europe is probably a function of the greater representation of migratory birds.

Another difference between my findings and those from Europe was the influence of fruiting plant diversity on frugivore biomass. This phenomenon has not been observed in Europe, probably because in temperate systems there are few fruiting species. In the more diverse subtropical environment of this study, where there were up to 19 fruiting species per site, the effect of fruiting plant diversity on frugivore biomass was similar to that of fruit biomass.

Effects of food availability, vegetation and primary productivity on bird abundance

Although food availability, vegetation and climate/primary productivity are known to be important influences on animal abundance (Andrewartha and Birch 1954, Evans et al. 2006, White 2008), few previous studies have compared their effects at a regional scale. Food (fruit and flower) availability was the dominant influence on bird abundance in the study region. Food explained 11.1% of the variation in total bird abundance; when feeding guilds were analysed separately, the explanatory power of food ranged from 8.3% (for insectivores) to 21.7% (for frugivores). Because fruit and flower availability differed among vegetation types, the association between vegetation and bird abundance was also strong. Vegetation explained 10.0% of the variation in total bird abundance; when feeding guilds were analysed separately, the explanatory power of vegetation ranged from 0.5% (for nectarivores) to 17.6% (for frugivores). Variables relating to primary productivity had only weak effects on bird abundance. Primary productivity explained 3.8% of the variation in total bird abundance; when feeding guilds were analysed separately, the explanatory power of primary productivity ranged from 1.9% (for nectarivores) to 4.9% (for insectivores). The values given above are likely to be underestimates, because the data were

vulnerable to stochastic variability, which may have accounted for the large residual components (57.8% - 69.2%) in the bird abundance models. When examining only spatial variation (which, with a mean 19 surveys per site and 39 per locality, was relatively immune from stochasticity), the models had greater explanatory power: food availability explained from 14.3% (for insectivores) to 58.4% (for frugivores) of the spatial variation in bird abundance.

The influence of food availability was greatest for frugivores and nectarivores, the guilds whose foods I measured, but even for all guilds combined, food (flowers and fruit) was a greater influence on abundance than was vegetation or productivity ó this despite the fact that fruit and/or nectar were important foods for only 32% of the individuals counted (I did not measure the availability of invertebrates, the main diet of the most numerous feeding guild). Fruit and flower availability also explained substantial amounts of variation in insectivore abundance. This might partly be due to the overlap among feeding guilds (fruit and nectar were important dietary items for 23% of the insectivores counted), and partly because nectar and fruit attract insects.

Given that primary productivity was an important influence on fruit and flower availability, and that food availability was the dominant influence on bird abundance, why was the relationship between productivity and abundance so weak? There was limited spatial variation in productivity during the study, but considerable temporal variation (coefficient of variation for GPP was 0.04 among sites, cf. 0.29 among months), suggesting that productivity influenced temporal rather than spatial patterns of food availability. Bird abundance showed the reverse pattern, with considerable spatial but limited temporal variation (spatial components comprised 26.1% of the total variation in bird abundance, cf. 4.5% for temporal components). These contrasting patterns have two implications. First, the number of migratory birds

entering the study region during times of high primary productivity must have been too small to match productivity-driven fluctuations in food availability. Second, the proportion of production consumed by birds must have varied spatially. For example, although productivity was relatively similar among vegetation types (mean productivity in the most productive habitat was only 1.06 times that in the least), bird abundance was not; this implies that a greater proportion of production was available as food for birds in some vegetation types (weedy regrowth, subtropical rainforest and wet sclerophyll forest) than in others. Meehan et al. (2004) found that the proportion of production consumed by birds in North America varied spatially, although not necessarily among vegetation types. The notion that differing proportions of primary production are available to birds in different habitats is not strongly supported by the handful of studies that have examined bird-community energetics in northern hemisphere deciduous and coniferous forests (e.g. Holmes and Sturges 1975, Alatalo 1978), but is untested for rainforests or eucalypt forests, the main vegetation types in the study region.

Most previous studies of productivity and bird abundance found a stronger relationship than I did, with productivity variables such as actual evapo-transpiration (Monkkonen et al. 2006, Symonds and Johnson 2008), temperature (Evans et al. 2006, Evans et al. 2008), Normalised Difference Vegetation Index (Hurlbert 2004), Net Primary Productivity (Meehan et al. 2004, Ding et al. 2005) and rainfall seasonality (Williams and Middleton 2008) explaining between 15-71% of the variation in bird numbers (cf. 1.9-13.9% in this study). With few exceptions, these studies were at continental or global scales comprehending substantial variation in productivity. In the only study at a scale smaller than this one (Ding et al. 2005), the annual

productivity of the poorest site was 0.33 that of the richest (cf. 0.75 for this study) due to the presence of a steep elevational gradient.

The weak productivity-abundance relationships I observed appear to have resulted from a combination of low spatial (but high temporal) variation in productivity and low temporal (but high spatial) variation in bird abundance. I would expect the relationship between productivity and bird abundance to be stronger in areas with greater spatial variation in productivity, or where long-distance migrants were a greater component of the avifauna.

Even when only spatial variation was considered, between 25.3% (for frugivores) and 57.2% (for insectivores) of the variation in abundance could not be explained by the models. What might account for this unexplained variation? Studies in eucalypt forests, the dominant vegetation type in the study region, have shown that foliar nutrients such as nitrogen, potassium, phosphorus and magnesium influence the abundance and/or species richness of arboreal marsupials (Braithwaite 1983, Cork and Catling 1996), arthropods (White 1993, Recher et al. 1996) and birds (Braithwaite et al. 1989, Recher et al. 1996). It is possible that foliar nutrient levels, which are related to soil characteristics, might account for much of the unexplained variation in bird abundance, probably through their effects on the biomass of folivorous arthropods.

A conceptual model of animal abundance

In the general introduction to this thesis I presented a conceptual model of the interactive effects on animal abundance of food, climate and vegetation. This study has examined the validity of aspects of this model and the strength of some of the posited relationships (Fig. 7.1). I found that food availability was the dominant influence on bird abundance, and that food was in turn influenced by productivity and

vegetation characteristics. The influence of climate/productivity on abundance was weak, apparently because vegetation characteristics determined the proportion of productivity available as food for birds.

My findings have prompted some alterations to the model presented in the general introduction. If climate were the only influence on vegetation, as in the first version of the model, then the influence of climate on bird abundance would have been much stronger than what was observed. In reality, vegetation characteristics such as floristics and structure are likely to be influenced by soil characteristics and historical factors (e.g. past climate, disturbance history, dispersal events etc.) more than by current climate.

An aspect of the model that merits further investigation is the nature of the effects of vegetation on food availability; foliar nutrient levels, which are in turn related to soil characteristics, might be an important influence on food availability for birds.

Conclusion

My study represents an important advance in our understanding of the factors that influence animal abundance over large areas. I showed that abundance is strongly influenced by food availability, which is in turn affected by climate, primary productivity and vegetation characteristics.

Few previous studies have compared spatial, temporal and spatio-temporal variation in regional bird abundance. I showed that, while most variation in abundance was spatial, spatio-temporal variation was also important, particularly for frugivores and nectarivores, which tracked seasonal changes in fruit and flower availability across the region. Seasonal variation in bird abundance among vegetation

types and localities needs to be considered in conservation planning, which is often

premised on species having static distributions.

Figure 7.1. A conceptual model of animal abundance. Thick red lines indicate strong influence; thin red lines indicate some influence; solid black lines indicate little influence; and dotted lines indicate relationships that were not examined. Food is the most important influence on animal abundance. Food availability is influenced by climate/productivity (which are closely linked, because productivity varies in response to spatio-temporal variation in climate) and vegetation characteristics, which determine the proportion of productivity available as food for animals. Vegetation characteristics may in turn be influenced by soil nutrients and historical factors. For the sake of clarity, some factors that were not examined, but which may be important influences on animal abundance (e.g. biotic interactions) have not been included.

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Appendices

Supplementary Table S1: Ranking of species for planting to conserve important frugivores, and as replacements for camphor laurels. Asterisks indicate exotic species.

Species	Family	Conservation value to important frugivores (wompoo and rose-crowned fruit-doves and topknot Pigeon) (scored from 1-17)	Value as a replacement for camphor laurel (scored from 1-17)
Ficus macrophylla	Moraceae	17	17
Ficus obliqua (= eugenioides)	Moraceae	17	17
Ficus rubiginosa (= platypoda)	Moraceae	17	17
Ficus superba var. henneana	Moraceae	17	17
Ficus virens (= infectoria)	Moraceae	17	17
Ficus watkinsiana	Moraceae	17	17
Acronychia oblongifolia	Rutaceae	16	15
Diploglottis cunninghamii (= australis)	Sapindaceae	16	14
Halfordia kendack	Rutaceae	15	15
Neolitsea australiensis	Lauraceae	15	15
Archontophoenix cunninghamiana	Arecaceae	15	14
Acronychia imperforata	Rutaceae	15	13
*Cinnamomum camphora**	Lauraceae	14	17
Cryptocarya erythroxylon	Lauraceae	14	15
Acronychia laevis	Rutaceae	14	14
Glochidion ferdinandi	Phyllanthaceae	14	14
Polyosma cunninghamii	Polyosmaceae	14	14

Solanum mauritianum*	Solanaceae	14	14
Syzygium ingens (= *Acmena brachyandra)*	Myrtaceae	14	14
Cananga odorata	Annonaceae	14	13
Decaspermum humile	Myrtaceae	14	13
Piper novaehollandiae	Piperaceae	14	13
Elaeocarpus grandis (= *angustifolius)*	Elaeocarpaceae	14	11
Pouteria queenslandica	Sapotaceae	14	11
Archontophoenix *alexandrae*	Arecaceae	13	14
Elaeocarpus reticulatus	Elaeocarpaceae	13	14
Olea paniculata	Oleaceae	13	14
Elaeocarpus kirtonii	Elaeocarpaceae	13	13
Ficus coronata (= *stephanocarpa)*	Moraceae	13	13
Galbulimima baccata (= *belgraveana)*	Himantandraceae	13	13
Syzygium smithii (= *Acmena smithii)*	Myrtaceae	13	13
Smilax australis	Smilacaceae	13	12
Cissus sterculiifolia	Vitaceae	13	10
Cryptocarya hypospodia	Lauraceae	13	10
Uvaria leichhardtii (= *Melodorum and* *Rauwenhoffia leichhardtii)*	Annonaceae	13	10
Cissus antarctica	Vitaceae	12	15
Ligustrum lucidum*	Oleaceae	12	15
Polyscias elegans	Araliaceae	12	15
Eriobotrya japonica*	Rosaceae	12	14

Acronychia acidula	Rutaceae	12	13
Pennantia cunninghamii	Pennantiaceae	12	13
Glochidion sumatranum	Phyllanthaceae	12	12
Melicope elleryana (= Euodia elleryana)	Rutaceae	12	12
Vitex lignum-vitae (= Premna lignum-vitae)	Lamiaceae	12	12
Litsea leefeana	Lauraceae	12	10
Alangium villosum subsp. polyosmoides	Cornaceae	12	9
Symplocos thwaitesii	Symplocaceae	12	9
Melia azedarach	Meliaceae	11	15
Cissus hypoglauca	Vitaceae	11	14
Schizomeria ovata	Cunoniaceae	11	14
Cayratia eurynema	Vitaceae	11	13
Ficus fraseri (= stephanocarpa and stenocarpa)	Moraceae	11	13
Harpephyllum caffrum*	Anacardiaceae	11	13
Ixora beckleri	Rubiaceae	11	13
Ehretia acuminata	Boraginaceae	11	12
Alphitonia excelsa	Rhamnaceae	11	11
Geitonoplesium cymosum	Luzuriagaceae	11	11
Guilfoylia monostylis	Surianaceae	11	11
Cryptocarya foetida	Lauraceae	11	9
Diospyros pentamera	Ebenaceae	11	9
Duboisia myoporoides	Solanaceae	11	9
Acronychia pauciflora	Rutaceae	11	8
Acronychia littoralis	Rutaceae	10	13
Legnephora moorei	Menispermaceae	10	13

Livistona australis	Arecaceae	10	13
Neolitsea dealbata	Lauraceae	10	13
Phytolacca octandra*	Phytolaccaceae	10	13
Polyscias murrayi	Araliaceae	10	13
Sloanea woollsii	Elaeocarpaceae	10	13
Strychnos psilosperma (= axillaris)	Loganiaceae	10	13
Tetrastigma nitens	Vitaceae	10	13
Podocarpus elatus	Araucariaceae	10	12
Streblus brunonianus (= pendulinus)	Moraceae	10	12
Cryptocarya microneura	Lauraceae	10	11
Pothos longipes	Araceae	10	11
Endiandra sieberi	Lauraceae	10	10
Syzygium oleosum	Myrtaceae	10	10
Cryptocarya bidwillii	Lauraceae	10	9
Rhodamnia rubescens	Myrtaceae	10	8
Syzygium corynanthum	Myrtaceae	10	8
Cinnamomum virens	Lauraceae	10	7
Litsea australis	Lauraceae	10	7
Micromelum minutum	Rutaceae	9	4
Cryptocarya glaucescens	Lauraceae	9	12
Cryptocarya mackinnoniana	Lauraceae	9	12
Diospyros fasciculosa	Ebenaceae	9	12
Ligustrum sinense*	Oleaceae	9	12
Syzygium australe	Myrtaceae	9	12
Acronychia wilcoxiana	Rutaceae	9	11
Cayratia clematidea	Vitaceae	9	11
Doryphora sassafras	Atherospermataceae	9	11

Syzygium crebrinerve	Myrtaceae	9	10
Hedycarya angustifolia	Monimiaceae	9	9
Dysoxylum rufum	Meliaceae	9	8
Myrsine variabilis	Primulaceae	9	8
Anthocarapa nitidula	Meliaceae	8	11
Beilschmiedia obtusifolia	Lauraceae	8	11
Drypetes deplanchei (= australasica)	Putranjivaceae	8	11
Endiandra hayesii	Lauraceae	8	11
Melicope micrococca (= Euodia micrococca)	Rutaceae	8	11
Myrsine howittiana	Primulaceae	8	11
Cryptocarya laevigata	Lauraceae	8	10
Cryptocarya rigida	Lauraceae	8	10
Cryptocarya obovata	Lauraceae	8	9
Cryptocarya williwilliana	Lauraceae	8	9
Elaeocarpus obovatus	Elaeocarpaceae	8	9
Endiandra discolor	Lauraceae	8	9
Endiandra muelleri	Lauraceae	8	9
Syzygium francisii	Myrtaceae	8	9
Archirhodomyrtus beckleri	Myrtaceae	8	8
Dysoxylum fraserianum	Meliaceae	8	8
Euroschinus falcatus	Anacardiaceae	8	8
Lantana camara*	Verbenaceae	8	8
Planchonella euphlebia	Sapotaceae	8	8
Rubus moorei	Rubiaceae	8	8
Acronychia pubescens	Rutaceae	8	7
Symplocos stawellii	Symplocaceae	8	7
Cryptocarya foveolata	Lauraceae	8	6
Cyclophyllum	Rubiaceae	8	6

longipetalum (= Canthium coprosmoides)			
Acronychia suberosa	Rutaceae	7	10
Diospyros australis	Ebenaceae	7	10
Psydrax odorata subsp. australiana (= Canthium odoratum)	Rubiaceae	7	10
Rhodamnia argentea	Myrtaceae	7	10
Acronychia baeuerlenii	Rutaceae	7	9
Canarium australasicum	Burseraceae	7	9
Cryptocarya macdonaldii (= sp. aff. cunninghamii)	Lauraceae	7	9
Gmelina leichhardtii	Lamiaceae	7	9
Cryptocarya meisneriana	Lauraceae	7	8
Maclura cochinchinensis	Moraceae	7	8
Litsea reticulata	Lauraceae	7	7
Owenia cepiodora	Meliaceae	6	7
Syzygium paniculatum	Myrtaceae	6	6
Citronella moorei	Cardiopteridaceae	6	9
Amylotheca dictyophleba	Loranthaceae	6	8
Cryptocarya triplinervis	Lauraceae	6	8
Beilschmiedia elliptica	Lauraceae	6	7
Cinnamomum oliveri	Lauraceae	6	7
Endiandra crassiflora	Lauraceae	6	3
Scolopia braunii	Salicaceae	5	4
Syzygium hemilamprum	Myrtaceae	5	5
Rhodamnia whiteana	Myrtaceae	5	7
Arytera foveolata	Sapindaceae	5	5
Trophis scandens (= Malaisia scandens)	Moraceae	5	5

Dysoxylum mollissimum	Meliaceae	5	4
Caelospermum paniculatum	Rubiaceae	4	2
Diploglottis campbellii	Sapindaceae	4	2
Balanops australiana	Balanopaceae	3	1
Citrus glauca	Rutaceae	3	1
Garcinia sp.	Clusiaceae	3	1
*Prunus sp.**	Amygdalaceae	3	1
Syzygium luehmannii	Myrtaceae	3	3

Supplementary Table S2: Nectar index.

Species	Gardens only?	Exotic?	Measured or estimated	Total flowers or inflorescences on-site	Total mass of birds feeding on flowers on-site (g)	Nectar index (g of bird per flower or inflorescence)	Comments
Acronychia imperforata			Measured	18 355	74.8	0.004	
Acronychia oblongifolia			Estimated			0.004	Assigned same score as *Acronychia imperforata*
Alloxylon flammeum	Yes	Yes	Measured	4 450 inflorescences	264	0.059	
Alloxylon pinnatum			Measured	230 inflorescences	0	0.002	Assigned half of score for *E. microcorys*
Amyema congener			Measured	250	0	0.029	Assigned same score as *Amyema* sp.
Amyema sp.			Measured	10 425	299	0.029	
Amylotheca dictyophleba			Measured	5 627	63	0.011	
Angophora costata			Measured	70	0	0.070	Assigned same score as *E. saligna*
Anigozanthos sp.	Yes	Yes	Estimated			0.490	Assigned same score as *Banksia* sp. (cultivated)
Anredera cordifolia		Yes	Measured	200	185	0.925	

Species			Method	Sample	Value 1	Value 2	Notes
Banksia integrifolia subsp. integrifolia			Measured	665 inflorescences	16802	25.266	
Banksia integrifolia subsp. monticola			Measured	1 778 inflorescences	3740	2.103	
Banksia plagiocarpa	Yes	Yes	Measured	8 inflorescences	203.4	6.143	Pooled Hinchinbrook and Banksia sp. (cultivated)
Banksia sp. (cultivated)	Yes	Yes	Measured	443 inflorescences	2567.1	6.143	Pooled Hinchinbrook and *Banksia* sp. (cultivated)
Banksia spinulosa			Measured	53 inflorescences	26	0.491	
Bauhinia x blakeana	Yes	Yes	Estimated			1.159	Assigned same score as *Melaleuca quinquenervia*
Benthamina alyxifolia			Measured	40	0	0.022	Assigned average of mistletoe values
Brachychiton acerifolius			Measured	70	0	0.070	Assigned same score as *E. saligna*
Callistemon sp.	Yes	?	Measured	5 333 inflorescences	1450.8	0.272	
Corymbia intermedia			Measured	3 345	1787.6	0.534	
Dendrophthoe vitellina			Measured	2 400	50	0.021	

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Species			Method			Score	Notes
Elaeocarpus reticulata			Measured	19 230	40	0.002	
Epacridaceae sp.			Estimated			0.008	Assigned same score as *Melichrus* sp.
Epacridaceae sp. (Cathedral Rock)			Measured	200	0	0.008	Assigned same score as *Melichrus* sp.
Erythrina variegata	Yes	Yes	Estimated			1.159	Assigned same score as *Melaleuca quinquenervia*
Erythrina x sykesii	Yes	Yes	Estimated			1.159	Assigned same score as *Melaleuca quinquenervia*
Eucalyptus acmenoides			Measured	3 470	0	0.070	Assigned same score as *E. saligna*
Eucalyptus ancophila or siderophloia			Measured	900	0	0.070	Assigned same score as *E. saligna*
Eucalyptus campanulata			Measured	1 750	0	0.004	
Eucalyptus grandis			Measured	30 950	11669	0.377	
Eucalyptus microcorys			Measured	4 335	16	0.004	
Eucalyptus nobilis			Estimated			0.070	Assigned same score as *E. saligna*
Eucalyptus pauciflora			Measured	11 45	18.7	0.016	

Eucalyptus pilularis			Measured	82 790	15851	0.191	
Eucalyptus resinifera			Measured	90	0	0.070	Assigned same score as *E. saligna*
Eucalyptus robusta			Measured	15 900	24601	1.547	
Eucalyptus saligna			Measured	2 755	179.5	0.065	
Eucalyptus sp. (unidentified stringybark)			Measured	5 150	472	0.092	
Eucalyptus sp. (unidentified)			Estimated			0.070	Assigned same score as *E. saligna*
Eucalyptus tereticornis			Measured	15	119	1.041	Small sample size led to unrealistically high score, so assigned score half way between *E. robusta* and *C. intermedia*
Grevillea robusta		Yes	Measured	4 285 inflorescences	13051	3.046	
Grevillea sp.	Yes	Yes	Measured	25 851 inflorescences	52624	2.036	
Grevillea sp. (prostrate)	Yes	Yes	Estimated			0.200	Assigned 0.1 of the score for *Grevillea* sp.
Hakea sp.	Yes	?	Estimated			0.490	Assigned same score as *Banksia* sp. (cultivated)

Jacaranda mimosifolia		Yes	Measured	8 700	8	0.016	Assigned same score as *E. pauciflora*
Kennedia rubicunda			Measured	120	0	0.008	Assigned same score as *Melichrus* sp.
Kniphofia uvaria	Yes	Yes	Estimated			0.008	Assigned same score as *Melichrus* sp.
Lambertia formosa	Yes		Estimated			0.490	Assigned same score as *Banksia* sp. (cultivated)
Lantana camara		Yes	Measured	41 707 inflorescences	384.8	0.009	
Lomatia sp.			Estimated			0.490	Assigned same score as *Banksia* sp. (cultivated)
Lonicera japonica		Yes	Measured	1 810	39	0.022	
Lophostemon confertus			Measured	5 820	0	0.002	Assigned half of score for *E. microcorys*
Melaleuca quinquenervia			Measured	32 31 inflorescences	3745.4	1.159	
Melaleuca sp. (large)	Yes	?	Estimated			1.159	Assigned same score as *Melaleuca quinquenervia*
Melaleuca sp. (small)	Yes	?	Estimated			0.580	Assigned half the score of *Melaleuca quinquenervia*

Species			Method				Comment
Melichrus sp.			Measured	12 668	100.6	0.008	
Mistletoe species			Measured	3 105	108	0.035	
Muellerina celastroides			Measured	1 119	111	0.099	
Muellerina eucalyptoides			Measured	3 000	216.2	0.072	
Salvia sp.	Yes	Yes	Measured	40 910	91	0.002	
Schefflera actinophylla	Yes	Yes	Estimated			1.159	Assigned same score as *Melaleuca quinquenervia*
Sphathodea campanulata	Yes	Yes	Estimated			1.159	Assigned same score as *Melaleuca quinquenervia*
Stenocarpus sinuatus			Measured	1 004	585.6	0.583	
Strelitzia reginae	Yes	Yes	Estimated			6.143	Assigned same score as *Banksia* sp. (cultivated)
Styphelia perileuca			Measured	1 790	0	0.008	Assigned same score as *Melichrus* sp.
Syncarpia glomulifera			Measured	930	0	0.004	
Syzygium australe			Measured	2 000	0	0.002	Assigned half of score for *E. microcorys*
Syzygium wilsonii	Yes	Yes	Measured	113	419.2	3.710	

| *Telopea speciosissima* | Yes | Measured | 8 inflorescences | 0 | 0.490 | Assigned same score as *B. spinulosa* |
| *Xanthorrhoea sp.* | | Measured | 6 inflorescences | 32 | 5.333 | |

Supplementary Table S3: Guild classifications of birds recorded on-site during study. Long-distance migrants are species of which all or most of the population leaves the study region for part of the year. All frugivores and nectarivores that are not specialists were classed as generalists.

Common name	Scientific name	Family	Weight (g)	Frugivore	Nectarivore	Insectivore	Specialist frugivore	Fruit nomad	Specialist nectarivore	Blossom nomad	Long-distance migrant
Australian Brush-turkey	*Alectura lathami*	Megapodiidae	2330.0	Yes		Yes					
Australian Wood Duck	*Chenonetta jubata*	Anatidae	808.0								
Straw-necked Ibis	*Threskiornis spinicollis*	Threskiornithidae	1351.5			Yes					
Square-tailed Kite	*Lophoictinia isura*	Accipitridae	587.0								
White-bellied Sea-eagle	*Haliaeetus leucogaster*	Accipitridae	2850.0								
Brown Goshawk	*Accipiter fasciatus*	Accipitridae	454.8								
Grey Goshawk	*Accipiter novaehollandiae*	Accipitridae	538.0								
Collared Sparrowhawk	*Accipiter cirrhocephalus*	Accipitridae	172.0								

Common name	Scientific name	Family	Mass								
Wedge-tailed Eagle	*Aquila audax*	Accipitridae	3660.0								
Bird of prey	*?*	Accipitridae	496.4								
White-headed Pigeon	*Columba leucomela*	Columbidae	420.0	Yes			Yes	Yes			
Brown Cuckoo-Dove	*Macropygia amboinensis*	Columbidae	237.0	Yes							
Emerald Dove	*Chalcophaps indica*	Columbidae	136.0	Yes							
Bar-shouldered Dove	*Geopelia humeralis*	Columbidae	129.0								
Wonga Pigeon	*Leucosarcia melanoleuca*	Columbidae	429.0	Yes							
Wompoo Fruit-Dove	*Ptilinopus magnificus*	Columbidae	455.0	Yes			Yes				
Rose-crowned Fruit-Dove	*Ptilinopus regina*	Columbidae	102.0	Yes			Yes	Yes			Yes
Topknot Pigeon	*Lopholaimus antarcticus*	Columbidae	538.0	Yes			Yes	Yes			
Yellow-tailed Black-Cockatoo	*Calyptorhynchus funereus*	Cacatuidae	766.0			Yes					
Rainbow Lorikeet	*Trichoglossus haematodus*	Psittacidae	132.0		Yes				Yes	Yes	

Common Name	Scientific Name	Family	Weight						
Scaly-breasted Lorikeet	*Trichoglossus chlorolepidotus*	Psittacidae	87.0		Yes			Yes	Yes	
Musk Lorikeet	*Glossopsitta concinna*	Psittacidae	76.0		Yes			Yes	Yes	
Australian King-Parrot	*Alisterus scapularis*	Psittacidae	209.0	Yes					
Crimson Rosella	*Platycercus elegans*	Psittacidae	115.0	Yes					
Eastern Rosella	*Platycercus eximius*	Psittacidae	105.8	Yes					
Brush Cuckoo	*Cacomantis variolosus*	Cuculidae	36.0			Yes				Yes
Fan-tailed Cuckoo	*Cacomantis flabelliformis*	Cuculidae	50.0			Yes				
Shining Bronze-Cuckoo	*Chrysococcyx lucidus*	Cuculidae	24.0			Yes				
White-throated Needletail	*Hirundapus caudacutus*	Apodidae	95.8			Yes				Yes
Azure Kingfisher	*Alcedo azurea*	Alcedinidae	33.5							
Laughing Kookaburra	*Dacelo novaeguineae*	Halcyonidae	354.0			Yes				
Sacred Kingfisher	*Todiramphus sanctus*	Halcyonidae	46.0			Yes				Yes

Dollarbird	*Eurystomus orientalis*	Coraciidae	123.3	Yes	Yes
Noisy Pitta	*Pitta versicolor*	Pittidae	99.0	Yes	
Superb Lyrebird	*Menura novaehollandiae*	Menuridae	1065.0	Yes	
White-throated Treecreeper	*Cormobates leucophaeus*	Climacteridae	21.0	Yes	
Red-browed Treecreeper	*Climacteris erythrops*	Climacteridae	24.5	Yes	
Superb Fairy-wren	*Malurus cyaneus*	Maluridae	10.0	Yes	
Variegated Fairy-wren	*Malurus lamberti*	Maluridae	8.0	Yes	
Spotted Pardalote	*Pardalotus punctatus*	Pardalotidae	8.0	Yes	
Striated Pardalote	*Pardalotus striatus*	Pardalotidae	11.7	Yes	
Yellow-throated Scrubwren	*Sericornis citreogularis*	Pardalotidae	17.0	Yes	
White-browed Scrubwren	*Sericornis frontalis*	Pardalotidae	13.0	Yes	
Large-billed Scrubwren	*Sericornis magnirostris*	Pardalotidae	10.0	Yes	

Common Name	Scientific Name	Family	Value						
Scrubwren (unidentified)	*Sericornis sp.*	Pardalotidae	13.3		Yes				
Brown Gerygone	*Gerygone mouki*	Pardalotidae	5.0		Yes				
Brown Thornbill	*Acanthiza pusilla*	Pardalotidae	7.0		Yes				
Buff-rumped Thornbill	*Acanthiza reguloides*	Pardalotidae	7.7		Yes				
Yellow Thornbill	*Acanthiza nana*	Pardalotidae	6.0		Yes				
Striated Thornbill	*Acanthiza lineata*	Pardalotidae	8.0		Yes				
Red Wattlebird	*Anthochaera carunculata*	Meliphagidae	131.0			Yes	Yes	Yes	Yes
Little Wattlebird	*Anthochaera chrysoptera*	Meliphagidae	67.8			Yes	Yes	Yes	Yes
Noisy Friarbird	*Philemon corniculatus*	Meliphagidae	101.0			Yes	Yes	Yes	Yes
Little Friarbird	*Philemon citreogularis*	Meliphagidae	67.0			Yes	Yes	Yes	Yes
Lewin's Honeyeater	*Meliphaga lewinii*	Meliphagidae	37.0	Yes		Yes	Yes		
Yellow-faced Honeyeater	*Lichenostomus chrysops*	Meliphagidae	17.0			Yes	Yes		
White-eared Honeyeater	*Lichenostomus leucotis*	Meliphagidae	23.6			Yes	Yes	Yes	

Brown-headed Honeyeater	*Melithreptus brevirostris*	Meliphagidae	15.7	Yes	Yes		
White-naped Honeyeater	*Melithreptus lunatus*	Meliphagidae	13.7	Yes	Yes		
Brown Honeyeater	*Lichmera indistincta*	Meliphagidae	10.3	Yes	Yes	Yes	
New Holland Honeyeater	*Phylidonyris novaehollandiae*	Meliphagidae	18.8	Yes	Yes	Yes	
White-cheeked Honeyeater	*Phylidonyris nigra*	Meliphagidae	18.7	Yes	Yes	Yes	
Eastern Spinebill	*Acanthorhynchus tenuirostris*	Meliphagidae	13.0	Yes	Yes	Yes	
Scarlet Honeyeater	*Myzomela sanguinolenta*	Meliphagidae	8.0	Yes	Yes	Yes	Yes
Scarlet Robin	*Petroica multicolor*	Petroicidae	12.9		Yes		
Rose Robin	*Petroica rosea*	Petroicidae	8.0		Yes		
Robin species	*Petroica sp.*	Petroicidae	15.1		Yes		
Pale-yellow Robin	*Tregellasia capito*	Petroicidae	14.0		Yes		
Eastern Yellow Robin	*Eopsaltria australis*	Petroicidae	20.0		Yes		
Logrunner	*Orthonyx temminckii*	Orthonychidae	60.0		Yes		

Eastern Whipbird	*Psophodes olivaceus*	Cinclosomatidae	62.0	Yes	
Varied Sittella	*Daphoenositta chrysoptera*	Neosittidae	12.0	Yes	
Crested Shrike-tit	*Falcunculus frontatus*	Pachycephalidae	29.0	Yes	
Golden Whistler	*Pachycephala pectoralis*	Pachycephalidae	24.0	Yes	
Rufous Whistler	*Pachycephala rufiventris*	Pachycephalidae	23.5	Yes	Yes
Little Shrike-thrush	*Colluricincla megarhyncha*	Pachycephalidae	36.6	Yes	
Little Shrike Thrush (possibly)	*Colluricincla megarhyncha?*	Pachycephalidae	50.3	Yes	
Grey Shrike-thrush	*Colluricincla harmonica*	Pachycephalidae	64.0	Yes	
Black-faced Monarch	*Monarcha melanopsis*	Dicruridae	23.0	Yes	Yes
Spectacled Monarch	*Monarcha trivirgatus*	Dicruridae	13.0	Yes	Yes
Leaden Flycatcher	*Myiagra rubecula*	Dicruridae	14.4	Yes	Yes

Satin Flycatcher	*Myiagra cyanoleuca*	Dicruridae	17.4			Yes			Yes
Flycatcher	*Myiagra sp.*	Dicruridae	17.2			Yes			
Rufous Fantail	*Rhipidura rufifrons*	Dicruridae	11.0			Yes			Yes
Grey Fantail	*Rhipidura fuliginosa*	Dicruridae	9.0			Yes			
Willie Wagtail	*Rhipidura leucophrys*	Dicruridae	21.0			Yes			
Spangled Drongo	*Dicrurus bracteatus*	Dicruridae	84.0	Yes	Yes	Yes			Yes
Black-faced Cuckoo-Shrike	*Coracina novaehollandiae*	Campephagidae	118.0			Yes			
Barred Cuckoo-Shrike	*Coracina lineata*	Campephagidae	100.0	Yes			Yes	Yes	Yes
White-bellied Cuckoo-Shrike	*Coracina papuensis*	Campephagidae	60.2			Yes			
Cicadabird	*Coracina tenuirostris*	Campephagidae	67.0			Yes			Yes
Varied Triller	*Lalage leucomela*	Campephagidae	33.0	Yes		Yes			
Olive-backed Oriole	*Oriolus sagittatus*	Oriolidae	95.0	Yes	Yes	Yes			
Figbird	*Sphecotheres viridis*	Oriolidae	138.0	Yes			Yes		
Grey Butcherbird	*Cracticus torquatus*	Artamidae	88.0			Yes			

Australian Magpie	*Gymnorhina tibicen*	Artamidae	304.0			Yes	
Pied Currawong	*Strepera graculina*	Artamidae	300.0	Yes		Yes	
Paradise Riflebird	*Ptiloris paradiseus*	Paradisaeidae	117.0	Yes		Yes	
Forest Raven	*Corvus tasmanicus*	Corvidae	663.0			Yes	
Torresian Crow	*Corvus orru*	Corvidae	551.0			Yes	
Green Catbird	*Ailuroedus crassirostris*	Ptilonorhynchidae	204.0	Yes		Yes	Yes
Regent Bowerbird	*Sericulus chrysocephalus*	Ptilonorhynchidae	99.0	Yes		Yes	Yes
Satin Bowerbird	*Ptilonorhynchus violaceus*	Ptilonorhynchidae	224.0	Yes		Yes	
Red-browed Finch	*Neochmia temporalis*	Passeridae	10.0				
Mistletoebird	*Dicaeum hirundinaceum*	Dicaeidae	9.0	Yes		Yes	Yes
Welcome Swallow	*Hirundo neoxena*	Hirundinidae	13.7			Yes	
Silvereye	*Zosterops lateralis*	Zosteropidae	10.0	Yes	Yes	Yes	
Bassian Thrush	*Zoothera lunulata*	Muscicapidae	109.5			Yes	

Russet-tailed Thrush	*Zoothera heinei*	Muscicapidae	83.0		Yes
Thrush species	*Zoothera sp.*	Muscicapidae	96.3		Yes

Supplementary Table S4: Mean numbers of flowers per inflorescence. Note:

Each inflorescence of Lantana *Lantana camara* was counted as only a single flower,

because birds seldom fed from Lantana inflorescences in relation to their abundance.

Plant species	Mean number of flowers per inflorescence	Source
Xanthorrhoea spp.	1188	(Lamont et al. 2000)
Banksia integrifolia subsp. integrifolia	1020	(McFarland 1985)
Banksia integrifolia subsp. monticola	1020	(McFarland 1985)
Banksia spinulosa	792	(McFarland 1985)
Melaleuca quinquenervia	50	(Pratt et al. 2005)
Grevillea robusta	40	(Kalinganire et al. 2000)

Site locations

Site number	Site ID (for csvs for modelling)	Easting (AGD 66, map zone 56)	Northing (AGD 66, map zone 56)	Vegetation type	Vegetation type (used in nectarivore analyses)	Location	Tenure	Comments
0	Site 1	473931	6640363	Subtropical rainforest	Subtropical rainforest	About 5 minutes walk from Dorrigo Rainforest Centre - at big Yellow Carabeen and Moreton Bay Fig about 50 m down left fork of Wonga Walk	Dorrigo National Park	Impossible to get good GPS reading due to heavy canopy
1	Site 2	474003	6640172	Subtropical rainforest	Subtropical rainforest	15-20 minutes walk from Dorrigo Rainforest Centre, at information sign (map) on lower Wonga Walk	Dorrigo National Park	Impossible to get good GPS reading due to heavy canopy
10	Site 5	495910	6635387	Wet sclerophyll	Wet sclerophyll	Centred on Forest Oak In gully south of firetrail, Pine Creek State Forest	Pine Creek State Forest	
11	Site 6	495486	6635472	Wet sclerophyll	Wet sclerophyll	In shallow gully of Bluegums north of firetrail, Pine Creek State Forest	Pine Creek State Forest	Clearfelled during study; replaced with Site 11b
11b	Site 42	496089	6635713	Wet	Wet sclerophyll	Just west of little-used firetrail	Pine Creek State	A replacement for site

				sclerophyll			Forest	11 (logged)
12	Site 7	506164	6632414	Subtropical rainforest	Subtropical rainforest	Centred on leaning Flooded Gum in littoral rainforest west of track to Bundagen Head	Bongil Bongil National Park	
12a	Site 43	441413	6623289	Wet sclerophyll	Wet sclerophyll	In eucalypt forest east of Cliffs Trail, centred on large *Eucalyptus nobilis*	New England National Park	
12RF	Site 44	506931	6633045	Subtropical rainforest	Subtropical rainforest	Just south of Bundagen Headland and west of track, centred on large Strangler-fig in Brush Box	Bongil Bongil National Park	Impossible to get good GPS reading due to heavy canopy
13	Site 8	505916	6631897	Dry sclerophyll	Coastal sclerophyll	In dune scrub just west of track to Bundagen Head	Bongil Bongil National Park	
13a	Site 45	441132	6622903	Temperate rainforest	Temperate rainforest	In temperate rainforest west of Cliffs Trail	New England National Park	
14	Site 9	505502	6631879	Subtropical rainforest	Coastal sclerophyll	In swamp forest / rainforest down hill (east) from lookout platform over Bundageree Creek on Bluff Loop walk	Bongil Bongil National Park	
14a	Site 46	470224	6627923	Dry sclerophyll	Dry sclerophyll	On steep slope east of Horseshoe Road; down hill near fallen tree	Baalijin Nature Reserve	
15	Site 10	470234	6628370	Dry	Dry sclerophyll	On trail-bike track on ridge just west of	Baalijin Nature	

				sclerophyll		Horseshoe Road	Reserve	
1626	Not used in analyses	467483	6632648	Garden	Garden	Garden of lower cabin, 1626 Darkwood Road	Private property	
18	Site 11	493951	6640322	Wet sclerophyll	Wet sclerophyll	Just south of Howards Road in Lantana and Flooded Gum forest	Bindarri National Park	
19	Site 12	494370	6640219	Subtropical rainforest	Subtropical rainforest	In rainforest north of Howards Road	Bindarri National Park	
20	Site 13	501436	6636004	Subtropical rainforest	Subtropical rainforest	In rainforest south of Hunters Road and east of unnamed tributary of Pine Creek	Bongil Bongil National Park	
21	Site 14	500974	6636276	Wet sclerophyll	Wet sclerophyll	In wet sclerophyll forest north of Hunters Road	Bongil Bongil National Park	
22	Site 15	462712	6643383	Dry sclerophyll	Dry sclerophyll	In dry sclerophyll forest downhill (west) from Johnsens Road, near bend in road	Private property	
23	Site 16	463132	6643392	Wet sclerophyll	Wet sclerophyll	In wet sclerophyll forest uphill (south) from Johnsens road	Private property	
26	Site 17	480610	6640584	Wet sclerophyll	Wet sclerophyll	Just east (uphill) of track near Never Never picnic area	Dorrigo National Park	Impossible to get good GPS reading due to heavy canopy

27	Site 18	480758	6641056	Temperate rainforest	Temperate rainforest	About 5 minutes from Never Never picnic area, down spur from bend In track towards Oreocallis Creek, about 40m from creek	Dorrigo National Park	Impossible to get good GPS reading due to heavy canopy
28a	Site 47	495259	6622481	Subtropical rainforest	Subtropical rainforest	In rainforest just south of firetrail and east of creek	Newry State Forest	
29a	Site 48	495730	6622477	Wet sclerophyll	Wet sclerophyll	In Blackbutt forest just south of firetrail	Newry State Forest	Logged after end of bird surveys, but before vegetation measurements could be taken
3 (ES)	Site 49	474687	6634433	Wet sclerophyll	Wet sclerophyll	About 20 minutes walk up track from Kathy's house on Tonaleah Community, 538 Darkwood Road - turn off track to right about 100 m above junction, and head down ridge about half way to unnamed (Joyce's) Creek	Bellinger River National Park	Impossible to get good GPS reading due to heavy canopy
30a	Site 50	476467	6621862	Dry	Dry sclerophyll	Down hill east of York Road, centred on	Gladstone State	

				sclerophyll		Grey Gum	Forest
31	Site 19	476003	6622015	Dry sclerophyll	Dry sclerophyll	Near big Turpentine in gully down hill (south) of York Road	Gladstone State Forest
32	Site 20	465484	6627770	Dry sclerophyll	Dry sclerophyll	On knoll north-west of Horseshoe Road	Baalijin Nature Reserve
33	Site 21	465824	6628071	Dry sclerophyll	Dry sclerophyll	On hillside south of Horseshoe Road, near huge hollowed-out dead tree	Baalijin Nature Reserve or Roses Creek State Forest
34	Site 22	478028	6628918	Wet sclerophyll	Wet sclerophyll	In gully east of Hospital Range Road	Scotchman State Forest
35	Site 23	477786	6628831	Dry sclerophyll	Dry sclerophyll	On slope west of Hospital Range Road	Scotchman State Forest
36	Site 24	505241	6632604	Dry sclerophyll	Coastal sclerophyll	In swamp forest near Bundageree Creek	Bongil Bongil National Park
36a	Site 51	463976	6627572	Dry sclerophyll	Dry sclerophyll	Down ridge west of Supply Road near Horseshoe Road	Baalijin Nature Reserve
37	Site 25	504892	6632376	Wet	Coastal	On slope north-west of disused firetrail	Bongil Bongil

				sclerophyll	sclerophyll		National Park	
37a	Site 52	464364	6627306	Dry sclerophyll	Dry sclerophyll	A little uphill (south) of Horseshoe Road	Baalijin Nature Reserve	
38	Site 26	457276	6622898	Wet sclerophyll	Wet sclerophyll	On steep slope south of Horseshoe Road	New England National Park	
39	Site 27	456876	6623070	Wet sclerophyll	Wet sclerophyll	On slope north of Horseshoe Road, just east of sharp bend	New England National Park	
44	Site 28	502383	6624282	Subtropical rainforest	Coastal sclerophyll	Pocket of littoral rainforest east of Urunga Lagoon	Crown Land	
45	Site 29	502378	6623834	Dry sclerophyll	Coastal sclerophyll	Just north of dirt road to "sandmines" beach, near Urunga Lagoon	Crown Land	
48	Site 30	483521	6627310	Subtropical rainforest	Subtropical rainforest	In rainforest north of Reids Creek Road	Gladstone State Forest	Impossible to get good GPS reading due to heavy canopy
49	Site 31	483782	6627363	Wet sclerophyll	Wet sclerophyll	In gully south of Reids Creek Road	Gladstone State Forest	
52	Site 32	476953	6638394	Subtropical rainforest	Subtropical rainforest	Near base of slope just north of unnamed tributary of Rosewood River; up hill a bit	Dorrigo National Park	Impossible to get good GPS reading due to

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						near big Ringwood		heavy canopy
53	Site 33	476683	6638452	Subtropical rainforest	Subtropical rainforest	Up ridge from Site 52; go up to big Flooded Gum where ridge begins to flatten, then turn right to young strangler-fig on big Brush Box	Dorrigo National Park	Impossible to get good GPS reading due to heavy canopy
538 Darkwood	Not used in analyses	474498	6633380	Garden	Garden	Garden of large house near "old bakery", 538 Darkwood Road	Private property	
54	Site 34	476776	6638886	Subtropical rainforest	Subtropical rainforest	In river-flat rainforest on Rosewood River; go north at leaning Quandong over pool; site is at small tree (White Booyong?) near big buttressed Carabeen	Dorrigo National Park	Impossible to get good GPS reading due to heavy canopy
55	Site 35	476435	6639118	Subtropical rainforest	Subtropical rainforest	In river-flat rainforest on Rosewood River; follow hill around to big fig near gully, then go a little toward river near twin Carabeens	Dorrigo National Park	Impossible to get good GPS reading due to heavy canopy
58	Site 36	486364	6630919	Dry sclerophyll	Dry sclerophyll	Just west of Milligans Trail (not marked on map)	Scotchman State Forest	
59	Site 37	486436	6631322	Wet	Wet sclerophyll	Just west of Milligans Trail (not marked on	Scotchman State	

				sclerophyll		map)	Forest	
60	Not used in analyses	474831	6635121	Subtropical rainforest	Subtropical rainforest	On unnamed tributary of Bellinger River (Joyce's Creek)	Bellinger River National Park	Impossible to get good GPS reading due to heavy canopy
60a	Site 53	486162	6625426	Wet sclerophyll	Wet sclerophyll	In Lantana 10m west of Woods Creek Road, about 60m after bridge over Woods Creek (or tributary)	Gladstone State Forest	
61	Not used in analyses	474945	6635440	Subtropical rainforest	Subtropical rainforest	On unnamed tributary of Bellinger River (Joyce's Creek)	Bellinger River National Park	Impossible to get good GPS reading due to heavy canopy
61a	Site 54	485906	6625087	Dry sclerophyll	Dry sclerophyll	On slope west of Woods Creek Road	Gladstone State Forest	
62	Site 38	461053	6615261	Subtropical rainforest	Subtropical rainforest	Leagues Scrub, just north of Horseshoe Road, before big viney treefall patch	New England National Park	Impossible to get good GPS reading due to heavy canopy
63	Site 39	460594	6615432	Subtropical rainforest	Subtropical rainforest	Leagues Scrub, just north of Horseshoe Road, past large stinging-trees	New England National Park	Impossible to get good GPS reading due to heavy canopy

64	Site 40	439940	6621405	Dry sclerophyll	Dry sclerophyll	Just uphill (east) of Cliffs Trail	New England National Park	
65	Site 41	440329	6621716	Wet sclerophyll	Wet sclerophyll	West of Cliffs Trail	New England National Park	
8	Site 3	474558	6634873	Subtropical rainforest	Subtropical rainforest	About 20 minutes walk up track from Kathy's house on Tonaleah Community, 538 Darkwood Road - just before track peters out, head down on left to rainforest flat along Joyce's Creek	Bellinger River National Park	Impossible to get good GPS reading due to heavy canopy
8a	Site 55	481504	6644685	Dry sclerophyll	Dry sclerophyll	On track to Killungoondie Plain, on knoll south of track	Dorrigo National Park	
9	Site 4	481915	6644499	Dry sclerophyll	Dry sclerophyll	On track to Killungoondie Plain, just south of track on top of small rise just before bridge over tributary of Wild Cattle Creek	Dorrigo National Park	
Bellingen Park	Not used in analyses	490054	6630766	Garden	Garden	Bellingen Park - site of Bellingen Markets	Crown Land	
Bindarri 1	Site 56	491783	6645816	Temperate rainforest	Temperate rainforest	Down slope north of Urumbilum Creek Road	Bindarri National Park	Impossible to get good GPS reading due to

								heavy canopy
Bindarri 2	Site 57	491485	6645579	Subtropical rainforest	Subtropical rainforest	Down slope near gully north-east of Urumbilum Creek Road	Bindarri National Park	Impossible to get good GPS reading due to heavy canopy
Bindarri 3	Site 58	491931	6648377	Temperate rainforest	Temperate rainforest	On slope north of track to Bangalow Creek Falls, about 200 m from picnic area	Bindarri National Park	Impossible to get good GPS reading due to heavy canopy
Bindarri 4	Site 59	492144	6648411	Temperate rainforest	Temperate rainforest	On slope west of track to Bangalow Creek Falls, about 200 m from falls	Bindarri National Park	Impossible to get good GPS reading due to heavy canopy
Boggy Creek Natives	Not used in analyses	484200	6633177	Garden	Garden	Garden of Colin Broadfoot's house on "Wonga" community, 178 Boggy Creek Road	Private property	
Bruxner 2	Site 60	509285	6654003	Subtropical rainforest	Subtropical rainforest	Near huge Flooded Gum on track through Bruxner Flora Reserve, about 80 m south of creek crossing on Swans Road	Orara East State Forest	Impossible to get good GPS reading due to heavy canopy
Bruxner1	Site 61	509119	6654241	Subtropical rainforest	Subtropical rainforest	Near big Brush Box with strangling fig on track through Bruxner Flora Reserve	Orara East State Forest	Impossible to get good GPS reading due to

								heavy canopy
Cam	Site 62	490314	6641339	Disturbed	Disturbed	On Promised Land Loop Road, just East of turn-off to "Lala Panzi"	Tuckers Knob State Forest	Impossible to get good GPS reading due to heavy canopy
Cam3	Site 63	488848	6638106	Disturbed	Disturbed	Centred on "Keep Out" Sign at Arthur Keogh Reserve, next to Never Never River	Crown Land	
Cooks 1	Site 64	472999	6621357	Subtropical rainforest	Subtropical rainforest	On slope above northern bank of Cooks Creek, about 150 m from ruined bridge	Juugawaarri Nature Reserve	Impossible to get good GPS reading due to heavy canopy
Cooks 2	Site 65	472745	6621482	Subtropical rainforest	Subtropical rainforest	On bend of Cooks Creek,near large Brush Box with strangler-fig north of creek	Juugawaarri Nature Reserve	Impossible to get good GPS reading due to heavy canopy
Coramba NR	Site 66	501792	6658859	Subtropical rainforest	Subtropical rainforest	On track from Coramba Oval to Orara River, near large Yellow Carabeen about 30m north of track	Coramba Nature Reserve	Impossible to get good GPS reading due to heavy canopy
CR1	Site 67	429489	6637680	Dry sclerophyll	Dry sclerophyll	Just east of track from Native Dog picnic area to Cathedral Rock, about 100m past 1st crossing over Native Dog Creek,	Cathedral Rock National Park	

						centred on flat granite slab		
CR2	Site 68	429298	6637242	Dry sclerophyll	Dry sclerophyll	Just west of track from Native Dog picnic area to Cathedral Rock, about 80 m past second crossing of Native Dog Creek	Cathedral Rock National Park	
Darkwood Cleavers Crossing	Site 69	466652	6632752	Disturbed	Disturbed	Clearing surrounded by Privet on "Dreamtime" community, about 50m east of Cleavers Crossing on Darkwood Road	Private property	
Darkwood Creek	Site 70	464942	6630987	Disturbed	Disturbed	Centred on bridge where Darkwood Road crosses Lenehans Creek	Private property	
Darkwood Plains Bridge	Site 71	467443	6632590	Disturbed	Disturbed	Eastern side of Plains Crossing on Darkwood Road	Private property	
Darkwood White Cedar	Site 72	464552	6631022	Disturbed	Disturbed	Centred on big white cedar about 300m east of Justins Bridge	Private property	
Ebor1	Site 73	436143	6636120	Dry sclerophyll	Dry sclerophyll	Just west of picnic area at end of road (Ebor Falls lower lookout)	Guy Fawkes River National Park	
Ebor2	Site 74	436518	6636004	Dry sclerophyll	Dry sclerophyll	In Snow Gum woodland south of road to Ebor Falls lower lookout	Guy Fawkes River National Park	
Evans	Not used in	512666	6654096	Garden	Garden	In Anne Evans garden on Jordans Way	Private property	Estimated from topo

	analyses					Korora		map
Gilmour	Not used in analyses	487600	6636271	Garden	Garden	In Phil Gilmour's garden on Rose's Road	Private property	Estimated from topo map
Kalang A	Site 75	478401	6624892	Disturbed	Disturbed	Bridge over unnamed tributary of Kalang River	Private property	
Kalang B (Hopsons Bridge)	Site 76	473029	6624935	Disturbed	Disturbed	Hopsons Bridge over Kalang River	Private property	
Maloney	Not used in analyses	489871	6625693	Garden	Garden	In Maureen Maloney's garden on Brierfield Road near South Arm Road	Private property	Estimated from topo map
Peguero	Not used in analyses	490346	6630876	Garden	Garden	In Gerard Peguero's garden on Hyde Street Bellingen	Private property	Estimated from topo map
Purslove	Not used in analyses	490140	6632141	Garden	Garden	In John Purslove's garden on Ringwood Place Bellingen	Private property	Estimated from topo map
River Track	Site 77	474498	6633380	Disturbed	Disturbed	Track down to river at 538 Darkwood Road	Private property	
Shambhala Bridge	Site 78	483147	6632551	Disturbed	Disturbed	Bridge over Boggy Creek on "Shambhala" community	Private property	
Simons	Not used in	490022	6640126	Garden	Garden	In Carol Simon's garden on Promised Land	Private property	Estimated from topo

	analyses					Loop Road		map
South Arm Road	Site 79	490115	6625837	Disturbed	Disturbed	Crossing over unnamed creek on South Arm Road, east of Brierfield Road	Private property	
Wonga1	Site 80	473867	6639531	Subtropical rainforest	Subtropical rainforest	Lower arm of Wonga Walk, centred on stag just past (south of) area of regrowth Giant Stinging-trees	Dorrigo National Park	Impossible to get good GPS reading due to heavy canopy
Wonga2	Site 81	474044	6639192	Subtropical rainforest	Subtropical rainforest	Lower arm of Wonga Walk, centred on large Brush Box about 300m north of Tristania Falls	Dorrigo National Park	Impossible to get good GPS reading due to heavy canopy
Woopi 1	Site 82	514019	6667757	Subtropical rainforest	Subtropical rainforest	On southern side of track to falls at Woolgoolga Flora Reserve, about 100m west of first creek crossing	Sherwood Nature Reserve	Impossible to get good GPS reading due to heavy canopy
Woopi 2	Site 83	513690	6667723	Subtropical rainforest	Subtropical rainforest	On northern side of track to falls at Woolgoolga Flora Reserve, just east of third creek crossing	Sherwood Nature Reserve	Impossible to get good GPS reading due to heavy canopy