

Fates of feathered fruit-eaters in fragmented forests

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ABSTRACT

Fruit-eating birds disperse many rainforest seeds, thereby influencing rainforest regeneration. The abundance of these birds may change following forest clearing, causing differences in seed dispersal between extensively-forested and fragmented areas. We assessed the responses of 26 frugivorous bird species to forest fragmentation by comparing their abundance among extensive tracts, remnants and regrowth patches of rainforest (16 replicate sites in each) in subtropical south-east Queensland, Australia. There were five species that were recorded in much lower numbers in remnants and/or regrowth than in extensive forest ("decreasers"), seven that showed higher abundance in remnants and/or regrowth than in extensive forest ("increasers") and 14 whose abundance did not change substantially between the three habitat types ("tolerant" species). The decreasers included three fruit-specialist rainforest pigeons (the wompoo, rose-crowned and superb fruit-doves *Ptilinopus magnificus*, *P. regina* and *P. superbus*). The increasers were largely bird species with mixed diets, many of which also use non-rainforest habitats. Two decreasers and two tolerant species were substantially more abundant during summer than winter whereas two increaser and two tolerant bird species were more abundant during winter. No effects of altitude on seasonal abundance were apparent. The results of this study show that fragmented remnant and regrowth patches of rainforest do not adequately conserve the full set of frugivorous avifauna. Furthermore, lower abundance of negatively-impacted birds in fragmented remnant and regrowth sites may lead to reduced regeneration of certain rainforest plant species due to a lack of seed dispersal in these habitats.

Key words: frugivore, birds, rainforest, fragmentation, seed dispersal, regeneration, altitude

Introduction

Birds that feed on fleshy fruits disperse the seeds of around 70% of plant species in Australian rainforests (Willson *et al.* 1989). This movement of seeds away from parent plants is considered to be a key contributor to plant community dynamics, reducing density-dependent seed and seedling mortality, transporting seeds to sites conducive to germination and survival, and contributing to the maintenance of plant genetic diversity (Howe and Smallwood 1982; Fleming *et al.* 1987; Chapman and Chapman 1995; Howe and Miriti 2000). The treatment of seeds by birds during feeding and digestion can also break seed dormancy, facilitating seedling germination (Howe and Smallwood 1982; van der Pijl 1982). Furthermore, avian seed dispersal enables fleshy-fruited rainforest plants to recruit to previously-cleared areas in disturbed landscapes (Uhl *et al.* 1982; Guevara *et al.* 1986; Gorchov *et al.* 1993; Guevara and Laborde 1993; Nepstad *et al.* 1996; Poschold *et al.* 1996; Duncan and Chapman 1999).

Changed numbers of frugivorous birds following forest clearing and fragmentation may result in altered seed dispersal and forest regeneration dynamics compared with natural forest systems (Janzen and Vasquez-Yanez 1991; Nepstad *et al.* 1996; Poschold *et al.* 1996; Thébaud and Strasberg 1997; Silva and Tabarelli 2000; Cordeiro and Howe 2001). Numbers of many frugivorous birds have declined worldwide following the fragmentation of tropical

rainforests (Johns 1991; Estrada *et al.* 1993; Kattan *et al.* 1994; Christensen and Pitter 1997; Restrepo *et al.* 1997; Warburton 1997; Renjifo 1999; Silva and Tabarelli 2000). Observations in subtropical Australia also indicate that numbers of some frugivorous birds have decreased following extensive clearing of rainforest, especially from lowland areas (Frith 1952; Date *et al.* 1991, 1996), but no systematic assessments of these changes have been undertaken.

Understanding the use of fragmented forests by birds in the context of extensive and ongoing forest clearing may help develop management strategies appropriate for avian conservation (Saunders *et al.* 1991). In the case of frugivorous birds, this knowledge may also contribute to the maintenance of the key ecological process of seed dispersal (Restrepo *et al.* 1997). The decline of particular frugivore species in fragmented landscapes may mean that certain plant species have lower dispersal potential in these areas. For example, Silva and Tabarelli (2000) describe a situation in which the frugivores capable of dispersing large fruits and seeds have declined in Brazilian forest fragments, and they predict the eventual extinction of such plants in the fragments.

In this paper we describe the responses of fruit-eating birds to forest fragmentation and associated vegetation changes in a subtropical Australian landscape. Specifically, we quantify the differences in frugivorous bird species numbers between

large tracts of forest, rainforest remnants and patches of rainforest regrowth. We also assess seasonal changes in the use of these rainforest habitats and investigate the potential for altitude to affect the birds' patterns of habitat use. We describe some implications of observed changes in the bird assemblage for the dispersal of large-seeded and other rainforest plants in fragmented landscapes.

Methods

Study sites

The study was conducted in subtropical rainforest within the Sunshine Coast and hinterland region, an area of approximately 4000 km² in south-east Queensland. Approximately two-thirds of the pre-European forest cover has been cleared throughout the region (Catterall *et al.* 1997), including extensive areas of rainforest (Meier and Figgis 1985; Young and McDonald 1987). Extant forests comprise a mosaic with cattle grazing land, agricultural cropland, plantation forests and suburban development.

Rainforest in coastal lowland areas of the study region had been almost totally cleared by the early 20th century (Frawley 1991). Except for patches within drier forests in the Cooloola area in the north, coastal lowland rainforest was basically reduced to scattered, small isolates behind coastal sand dunes or fringing watercourses. Subcoastal lowlands associated with the Mary River Valley approximately 30 kilometres inland had also been cleared, mostly for cattle grazing. The remainder of the study region comprises undulating terrain associated with the Blackall and Conondale Ranges. Rainforest was cleared from the basaltic plateau of the more easterly Blackall Range, firstly for timber and then for dairy farming (Frawley 1991), leaving rainforest remnants in gullies and along steeper slopes of the Blackall Range (Figure 1). Extensive eucalypt forest-rainforest mosaics cover the northern and southern ends of the Blackall Range and large areas of the Conondale Ranges. Unmanaged rainforest regrowth on previously-cleared land now contributes to regional forest cover. Additionally, many small plots have been replanted by private landholders, community groups and local authorities over the past three decades (Catterall *et al.* 2004).

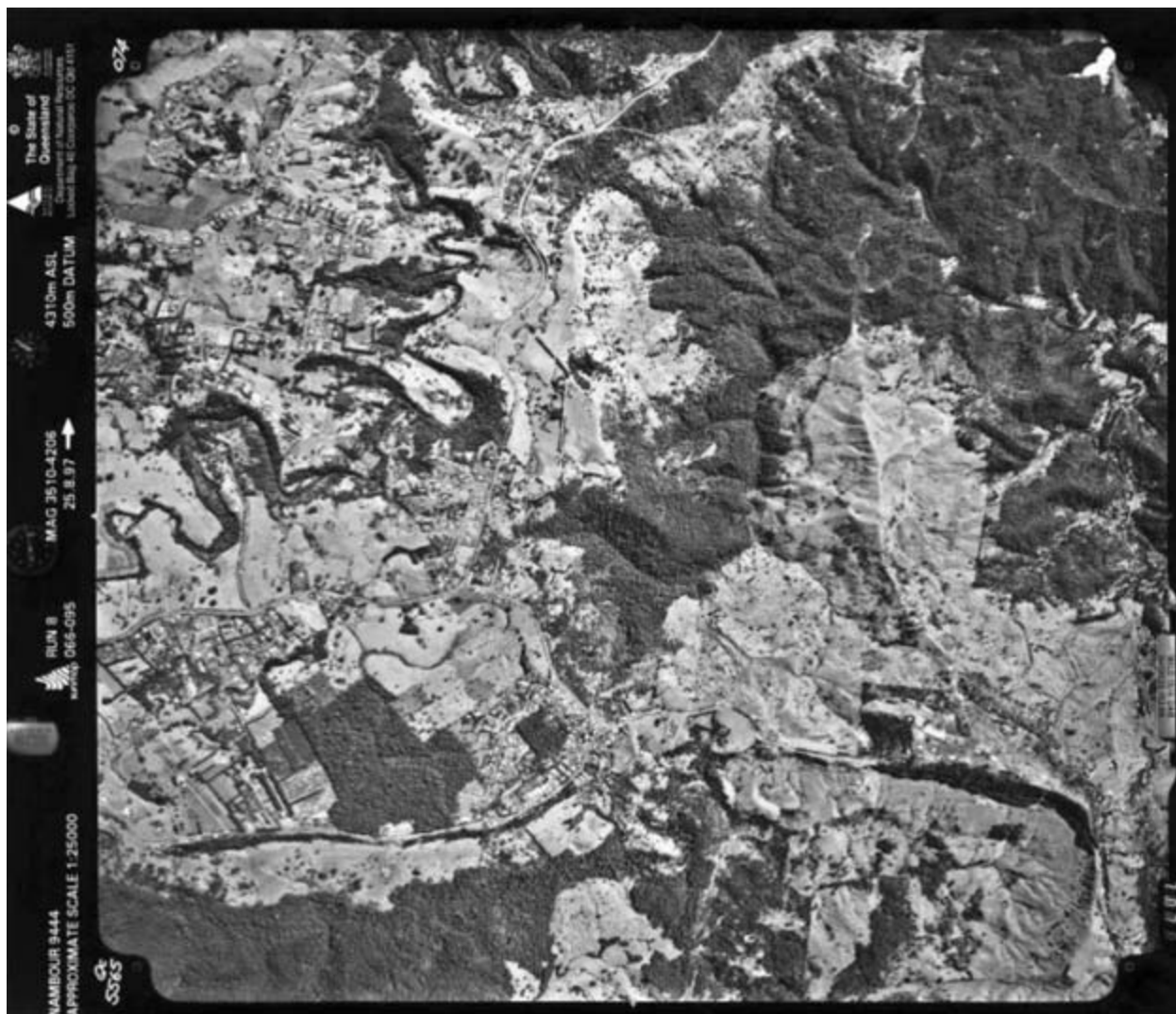


Figure 1. Aerial view of part of the Blackall Range showing remnant and regrowth forests interspersed with rural and residential landuses (Source: Queensland Department of Natural Resources, 1997). Forest cover tends to be associated with undulating terrain or watercourses. The area seen in this view contains a moderate level of forest cover compared with other fragmented parts of the landscape.

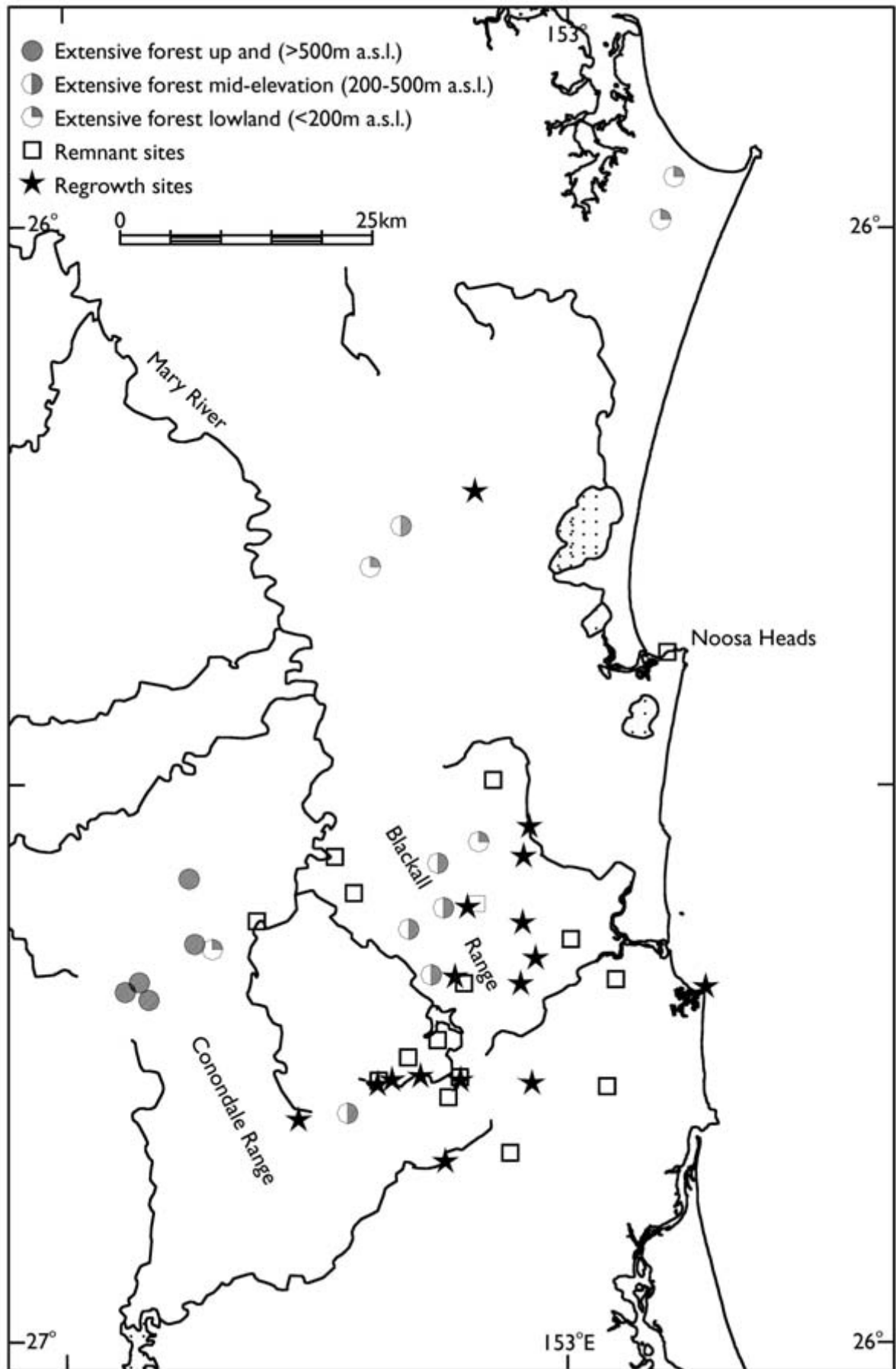


Figure 2. Map of study region showing site locations in relation to the coast, watercourses and major waterbodies.

Study sites were chosen to represent a range of situations in which rainforest remains or has re-established in the study region. We selected 16 replicate sites within each of three different states of rainforest landscape context and condition: (i) rainforest within extensive tracts of forest; (ii) remnant rainforest isolated from extensive forest by surrounding cleared and modified land; and (iii) regrowth, also isolated by cleared and modified land. Sites were identified using vegetation mapping, aerial photography and on-ground assessment. As far as possible, replicate sites within each type were distributed throughout the study region. A one-hectare plot was marked within each of the study sites. The configuration of the plot was influenced by the shape and landform attributes of each site, but was usually either 200m x 50m or 100m x 100m.

Extensive forest sites were distributed along eastern slopes of the Conondale Ranges in the west of the study region, on the northern and southern ends of the Blackall Range, and on the Cooloola sand mass in the north (Figure 2). These sites were located within forest tracts greater than 4000 ha in size and comprising at least 20% rainforest. The balance of these tracts was eucalypt open forest and woodland together with some large areas of forest timber plantations, usually the native hoop pine *Araucaria cunninghamii* or the introduced slash pine *Pinus elliotii*.

Remnant and regrowth sites were thoroughly interspersed with one another throughout the study region and were located within a matrix of predominantly rural and semi-rural land uses. There were fewer patches of rainforest in the landscapes surrounding remnant and regrowth sites than were found throughout extensive forest mosaics. Regrowth sites were often situated in more highly cleared parts of the landscape than remnant sites. The mean size of remnant sites, including contiguous eucalypt forest, was approximately 46.1 ha (range 2-100 ha, standard error 9.4 ha) and for regrowth sites was 3.4 ha (range 2-10 ha, S.E. 0.5 ha).

The sixteen extensive forest sites were stratified by altitude: five were located in upland (>500 m a.s.l.), six in mid-elevation (200-500 m a.s.l.) and the remaining five in lowland (<200 m a.s.l.) forests (overall range 90-800 m, mean 370 m, S.E. 53 m a.s.l.). Remnants and regrowth were located at mid-elevations and in lowland areas (both ranging from 20-500 m a.s.l., with mean 206 m, standard error 41 m; and mean 165 m, standard error 41 m, respectively).

Efforts were made to include a similar range of fruiting plants within plots across extensive and remnant sites to concentrate on the influence of landscape situation rather than resource differences. Extensive and remnant sites typically contained the following fleshy-fruited plant taxa: palms (e.g. *Archontophoenix cunninghamiana* and *Livistona australis*), figs *Ficus* spp., laurels (especially *Cryptocarya* spp. and *Endiandra* spp.), Elaeocarpaceae (*Elaeocarpus* and *Sloanea* spp.), basswoods (especially *Polyscias* spp.), Sapotaceae (e.g. *Pouteria* spp.), Sapindaceae (e.g. *Diploglottis australis*) and fleshy-fruited Myrtaceae (e.g. *Syzygium* and *Acmena* spp.). Fleshy-fruited vines, especially the native grapes (*Cissus* spp.), whipvine *Flagellaria indica* and climbing pandans *Freyinetia* spp. were common throughout extensive and isolated remnant sites. Some remnant sites seemed to contain a greater proportion of pioneer species such as bleeding heart *Homalanthus nutans*, blackwood

wattle *Acacia melanoxylon*, macaranga *Macaranga tanarius* and fleshy-fruited weeds (from the Lauraceae, Oleaceae, Solanaceae and Verbenaceae families) than most extensive sites, usually in areas of ongoing disturbance, such as around walking tracks.

Rainforest regrowth sites were dominated by pioneer and early-successional plant species, including a variety of invasive fleshy-fruited weeds. Regrowth sites commonly contained sandpaper figs (*Ficus coronata* and *F. fraseri*), jackwood *Cryptocarya glaucescens*, bleeding heart *Homalanthus nutans*, basswood *Polyscias elegans*, wild quince *Guioa semiglaucata*, piccabean palms *Archontophoenix cunninghamiana* and the introduced woody weeds camphor laurel *Cinnamomum camphora*, broad- and small-leaved privet *Ligustrum lucidum* and *L. sinense*, wild tobacco *Solanum mauritianum* and lantana *Lantana camara*. Fleshy-fruited vines were also common.

Bird surveys

Our quantitative measure of bird abundance was the number of individuals of each frugivorous bird species seen or heard during a 40 minute visit to each 1-hectare plot. Bird counts were conducted within four hours of dawn and involved walking throughout the plot as many times as possible, following up on movements and sounds of falling fruit. All sites were surveyed by the same observer (Moran). Bird surveys were not conducted during strong wind or heavy rain. Small, canopy-dwelling species (e.g. mistletoebird) may have been under-recorded if they were not calling.

Each plot was surveyed in this manner on four separate occasions; twice during January-March (summer) and twice between July and September (winter) in 2001. Consecutive surveys at any site were no less than three weeks apart. The total observation time at each site was 160 minutes; 80 minutes in both summer and winter.

Data treatment

The number of individuals of each frugivorous bird species was summed across the two visits made during a season. Data for species that were recorded in less than five sites in both seasons were not analysed for this part of the study. A two-way split plot Analysis of Variance (ANOVA) was used to test whether the abundance of birds that were recorded in at least five sites during both seasons varied between site types (three levels) and seasons (two levels). Season was used as the split, with site nested within site type (site:site type) as the error term when testing for effect of site type, and site:site type x season as the error term when testing for the effect of season or the interaction between season and site type. Where a species was recorded in at least five sites during one season only, a one-way ANOVA was conducted on the data from only that season to test for an effect of site type on abundance, and a paired t-test was used to test whether the difference in numbers between seasons was significant. A species was considered to show a substantial difference in numbers between summer and winter if the ANOVA result was significant and the abundance turnover exceeded 50% (after Catterall *et al.* 1998). The method used to calculate seasonal turnover was:

$$\text{percent abundance turnover} = \frac{(\text{max.} - \text{min.})}{\text{max.}} \times 100$$

Table 1 Frugivorous bird species recorded in this study. Nomenclature and order follow Christidis and Boles (1994) († indicates seed grinder (likely to destroy seeds) and * indicates introduced species). Sites indicates the number of sites (out of 48) in which the species was recorded in summer (two surveys), winter (two surveys) and across all surveys. Analyses shows species that were analysed statistically (+).

Common name	Scientific name	Sites:			Analyses
		summer	winter	all surveys	
Australian brush-turkey†	<i>Alectura lathami</i>	16	14	23	+
rock dove†*	<i>Columba livia</i>	0	1	1	
white-headed pigeon†	<i>Columba leucomela</i>	16	13	22	+
brown cuckoo-dove†	<i>Macropygia amboinensis</i>	40	37	42	+
emerald dove†	<i>Chalcophaps indica</i>	12	8	15	+
bar-shouldered dove†	<i>Geopelia humeralis</i>	15	16	23	+
wonga pigeon†	<i>Leucoscarcia melanoleuca</i>	3	3	5	
wompoo fruit-dove	<i>Ptilinopus magnificus</i>	18	20	25	+
superb fruit-dove	<i>Ptilinopus superbus</i>	12	1	13	+
rose-crowned fruit-dove	<i>Ptilinopus regina</i>	36	6	36	+
topknot pigeon	<i>Lopholaimus antarcticus</i>	5	1	6	+
galah†	<i>Cacua roseicapilla</i>	2	1	3	
sulphur-crested cockatoo†	<i>Cacatua galerita</i>	8	14	16	+
rainbow lorikeet†	<i>Trichoglossus haematodus</i>	29	22	32	+
scaly-breasted lorikeet†	<i>Trichoglossus chlorolepidotus</i>	4	3	7	
Australian king-parrot†	<i>Alisterus scapularis</i>	12	18	23	+
crimson rosella†	<i>Platycercus elegans</i>	3	1	4	
pale-headed rosella†	<i>Platycercus adscitus</i>	4	10	14	+
common koel	<i>Eudynamis scolopacea</i>	17	0	17	+
channel-billed cuckoo	<i>Scythrops novaehollandiae</i>	7	0	7	+
little wattlebird	<i>Anthochaera chrysoptera</i>	0	6	6	+
noisy friarbird	<i>Philemon corniculatus</i>	0	3	3	
blue-faced honeyeater	<i>Entomyzon cyanotis</i>	0	1	1	
noisy miner	<i>Manorina melanocephala</i>	3	1	3	
Lewin's honeyeater	<i>Meliphaga lewinii</i>	48	48	48	+
scarlet honeyeater	<i>Myzomela sanguinolenta</i>	17	26	33	+
black-faced cuckoo-shrike	<i>Coracina novaehollandiae</i>	3	10	10	+
barred cuckoo-shrike	<i>Coracina lineata</i>	2	0	2	
varied triller	<i>Lalage leucomela</i>	2	2	4	
olive-backed oriole	<i>Oriolus sagittatus</i>	1	1	2	
figbird	<i>Sphecotheres viridis</i>	31	36	41	+
grey butcherbird	<i>Cracticus torquatus</i>	2	2	4	
Australian magpie	<i>Gymnorhina tibicen</i>	18	20	26	+
pied currawong	<i>Strepera graculina</i>	23	35	38	+
paradise riflebird	<i>Ptiloris paradiseus</i>	4	3	5	
Torresian crow	<i>Corvus orru</i>	20	34	35	+
green catbird	<i>Ailuroedus crassirostris</i>	32	28	35	+
regent bowerbird	<i>Sericulus chrysocephalus</i>	1	4	5	
satin bowerbird	<i>Ptilonorhynchus violaceus</i>	7	2	7	+
house sparrow†*	<i>Passer domesticus</i>	0	1	1	
mistletoebird	<i>Dicaeum hirundinaceum</i>	3	2	5	
silveryeye	<i>Zosterops lateralis</i>	4	18	20	+

Table 2. Frugivorous bird species abundance in each of the three site types, during summer and winter. The mean abundance of individuals (summed across two 40-minute surveys in 1 ha) is shown for all sites (Total), in Extensive forest (Ext, 16 sites), Remnants (Rem, N=16), and Regrowth (Reg, N=16). ANOVA *P* shows results of analyses testing for differences in abundance between site types (ST), seasons (S) and ST×S. x indicates season for which effect of site type was not tested (species too infrequent). Letters next to means show LSD results (means with different letters are significantly different). Abund. pattern corresponds with Fig. 1 (i to iii are “decreasers”, iv to vi “increasers”, and vii “tolerant”).

Bird species	Season	Mean abundance				ANOVA <i>P</i> values			Abund. pattern
		Total	Ext	Rem	Reg	ST	S	ST × S	
Australian brush-turkey	s	0.63	0.44	0.82	0.63	0.35	0.17	0.96	vii
	w	0.38	0.13	0.56	0.44				
white-headed pigeon	s	0.63	0.38	0.88	0.63	0.10	0.55	0.11	vii
	w	0.77	0.19	0.63	1.50				
brown cuckoo-dove	s	2.04	2.75a	2.63a	0.75b	0.02	0.20	0.06	iii
	w	2.46	2.06	3.63	1.69				
emerald dove	s	0.42	0.25	0.56	0.44	0.43	0.07	0.89	vii
	w	0.23	0.13	0.38	0.19				
bar-shouldered dove	s	0.52	0.00b	0.88a	0.69a	0.002	0.67	0.29	iv
	w	0.46	0.00	0.50	0.88				
wompoo fruit-dove	s	1.21	2.65a	1.00b	0.00c	0.0002	0.87	0.71	i
	w	1.25	2.65	0.82	0.31				
superb fruit-dove	s	0.29	0.56a	0.25ab	0.06b	0.03 ¹	0.0012 ²		ii
	w	0.02	0.00	0.06	0.00	x			
rose-crowned fruit-dove	s	1.88	2.81a	2.00b	0.81c	0.002 ¹	0.0001	0.04	i
	w	0.23	0.56	0.13	0.00	0.07 ¹			
topknot pigeon	s	0.44	1.06	0.06	0.19	0.24 ¹	0.33 ²		vii
	w	0.15	0.00	0.00	0.44	x			
sulphur-crested cockatoo	s	0.35	0.56	0.31	0.19	0.07	0.54	0.08	vii
	w	0.42	0.94	0.13	0.19				
rainbow lorikeet	s	2.52	1.81b	1.19b	4.56a	0.01	0.08	0.16	v
	w	1.73	0.94	1.50	2.75				
Australian king-parrot	s	0.35	0.38	0.38	0.32	0.31	0.17	0.34	vii
	w	0.65	1.06	0.63	0.26				
pale-headed rosella	s	0.15	0.25	0.19	0.00	x			
	w	0.69	0.00	0.75	1.31	0.10 ¹	0.36 ²		vii
common koel	s	0.48	0.38	0.38	0.69	0.40 ¹	0.0001 ²		vii
	w	0.00	0.00	0.00	0.00	x			
channel-billed cuckoo	s	0.17	0.06	0.19	0.25	0.46 ¹	0.01 ²		vii
	w	0.00	0.00	0.00	0.00	x			
little wattlebird	s	0.00	0.00	0.00	0.00	x			
	w	0.15	0.00	0.18	0.25	0.21 ¹	0.02 ²		vii
Lewin's honeyeater	s	4.29	4.13	4.75	4.00	0.46	0.04	0.53	vii
	w	3.79	3.88	3.88	3.63				
scarlet honeyeater	s	0.60	1.00	0.56	0.25	0.06 ¹	0.12	0.03	vii
	w	0.92	0.56	1.13	1.06	0.27 ¹			
black-faced cuckoo-shrike	s	0.08	0.00	0.00	0.25				
	w	0.60	0.13b	0.06b	1.63a	0.006 ¹	<0.0001 ²		v
figbird	s	3.60	1.00b	2.56b	7.25a	0.0006	0.26	0.81	v
	w	4.96	1.56	4.94	8.38				
Australian magpie	s	1.40	0.00c	1.00b	3.19a	<0.0001	0.31	0.17	vi
	w	1.08	0.13	1.06	2.06				
pied currawong	s	0.98	0.88	1.06	1.00	0.42	0.0004	0.40	vii
	w	2.31	1.88	3.06	2.00				
Torresian crow	s	1.04	0.25b	0.82b	2.06a	0.0001	0.02	0.81	v
	w	1.85	1.19	1.32	3.06				
green catbird	s	1.58	1.94a	2.44a	0.38b	0.0001	0.55	0.89	iii
	w	1.46	1.81	2.19	0.38				
satin bowerbird	s	0.19	0.13	0.19	0.25	0.75 ¹	0.45 ²		vii
	w	0.10	0.06	0.00	0.25	x			
silveryeye	s	0.42	0.00	0.00	1.25	x			
	w	2.59	1.06b	1.69b	5.00a	0.03 ¹	0.002 ²		v

¹*P* value from single-factor ANOVA testing site type effect within season

²*P* value from paired t-test of difference between seasons; all other *P* values from two-way ANOVA

Where: **max.** is number of individuals recorded in the season in which the species was most common; and

min. is the number in the season in which it was least common.

Where there was a significant effect of site type, Least Significant Difference (LSD) comparisons were conducted to test for pairwise differences. ANOVA procedures and LSD tests were conducted using the SAS statistical package (SAS Institute 1999).

We tested for an interaction between site elevation (three levels: high (N=5), mid (N=6) or low (N=5)) and season (two levels: summer and winter) on selected frugivorous bird numbers in extensive forest by way of a two-factor ANOVA using the PROC GLM procedure in SAS (SAS Institute 1999). We conducted analyses on pooled data for all frugivorous birds and separately on data for selected species (those nominated as being altitudinal migrants by Date *et al.* 1991).

Classification of frugivorous birds

Literature searches revealed records of many bird species consuming fleshy fruit. As pointed out by Jones and Crome (1990), almost any rainforest-dwelling vertebrate will occasionally eat fleshy fruit, although some species do so very rarely. We used reference texts to systematically classify frugivorous species. Bird species recorded during our surveys were considered frugivores if they had been described as eating fruit in Blakers *et al.* (1984), or they were recorded in Barker and Vestjens (1988, 1989) or the *Handbook of Australian, New Zealand and Antarctic Birds* (HANZAB) series (Marchant and Higgins 1993; Higgins and Davies 1996; Higgins 1999; Higgins *et al.* 2001) consuming fruits or seeds of fleshy-fruited plants from more than three genera. Parrots, lorikeets and rosellas (Green 1993) and some pigeons (Frith 1982) grind or crush many, if not most of the seeds from the fleshy fruits they consume. Although such birds may have relatively low potential as seed dispersers, they were included in the list of avian frugivores if they satisfied the previous criteria.

Results

In total, 2768 individuals from 42 bird species that were considered to be frugivores in south-east Queensland were recorded during the study. Other species that are known to eat fruit infrequently were recorded during surveys but these did not meet the stated criteria and are not considered further in this paper. Of the 42 frugivorous bird species recorded in our surveys, 26 were sufficiently common (present at five or more sites in at least one season) for statistical analyses. Table 1 lists all frugivorous bird species recorded during our surveys, the number of sites in which each was recorded during summer and winter, and whether or not it was included in statistical analyses.

The species for which data were statistically analysed are listed in Table 2, along with the mean number of individuals of the species overall and in each of the three

site types during summer and winter, and the results of statistical tests for differences between site types and seasons. Twelve of the 42 species showed a statistically significant ($P < 0.05$) difference in abundance among the three site types in one or both seasons. Each species' response pattern is also indicated in Table 2. Eight species showed a significant difference between seasons together with greater than 50% seasonal turnover in abundance. The rose-crowned fruit-dove *Ptilinopus regina* and scarlet honeyeater *Myzomela sanguinolenta* showed a significant interaction between site type and season.

Patterns of statistically significant differences in abundance between site types (Table 3, Figure 3) grouped readily into three classes:

1. **decreasers:** species that showed lower numbers in regrowth than extensive forest areas, with numbers in remnants intermediate or resembling extensive forest;
2. **increasers:** species that showed higher numbers in regrowth than extensive forest, with numbers in remnants intermediate or resembling regrowth; and
3. **tolerant:** no significant difference in numbers between remnants, regrowth and extensive forest.

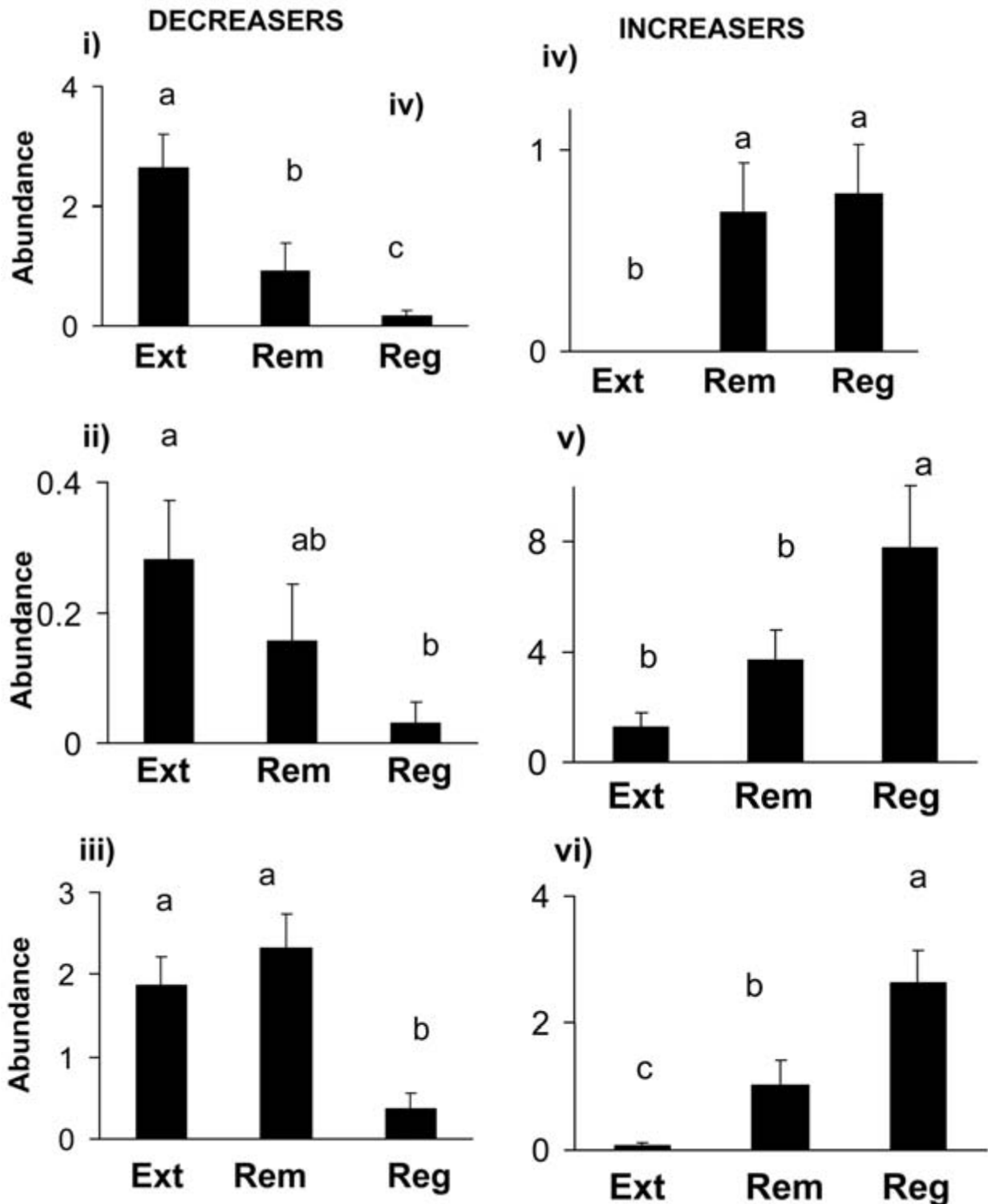
Table 3. Frugivorous bird species' responses to rainforest fragmentation, and their seasonality. Numerals (i-vii) show the pattern of abundance change among the three site types (see text, Fig. 1 and Table 2); Season shows the time of greater abundance if the effect of season was significant and turnover exceeded 50%. † indicates seed grinder (likely to destroy seeds).

	Species	Season
Decreasers	i wompoo fruit-dove	
	rose-crowned fruit-dove	summer
	ii superb fruit-dove	summer
	iii brown cuckoo-dove†	
Increasesers	iv bar-shouldered dove†	
	rainbow lorikeet†	
	black-faced cuckoo-shrike	winter
	v figbird	
	Torresian crow	
	silveryeye	winter
Tolerant	vi Australian magpie	
	Australian brush-turkey†	
	white-headed pigeon†	
	emerald dove†	
	topknot pigeon	
	sulphur-crested cockatoo†	
	Australian king-parrot†	
	vii pale-headed rosella†	
	common koel	summer
	channel-billed cuckoo	summer
	little wattlebird	winter
Lewin's honeyeater		
scarlet honeyeater		
ped currawong	winter	
satin bowerbird		

There were five decreaser species (Table 3), three of which were fruit-doves (*Ptilinopus* spp.). The fruit-doves generally showed declining abundance from extensive forest through remnants to regrowth (Table 2, Figure 3). The other two decreasers, the brown cuckoo-dove and green catbird, showed similar abundance in extensive and remnant forests but were less common in regrowth (Table 2, Figure 3). There were seven increaser species, five of which (rainbow lorikeet, black-faced cuckoo-shrike, figbird, Torresian crow and silvereye) were significantly more abundant in regrowth than in either remnant or extensive forest (Table 2, Figure 3). The increaser bar-

shouldered dove showed similar abundance between remnant and regrowth sites and was absent from extensive forest, while the Australian magpie was least abundant in extensive forest, and most abundant in regrowth, with numbers in remnant forest intermediate (Table 2, Figure 3). The abundance of the remaining 14 species did not differ significantly among site types.

The common koel and channel-billed cuckoo were substantially more abundant during summer than in winter, clearly the result of immigration, and the rose-crowned and superb fruit-doves also showed large and



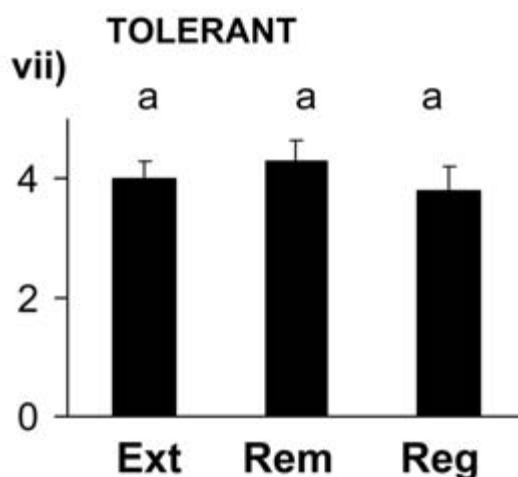


Figure 3. Selected bird species showing examples of the seven patterns of response to rainforest fragmentation. Abundance (average of summer and winter data) shows mean and standard error. Ext = Extensive forest tracts; Rem = Remnant forest; and Reg = Regrowth patches; i) wompoo fruit-dove, ii) superb fruit-dove, iii) green catbird, iv) bar-shouldered dove, v) figbird, vi) Australian magpie, and vii) Lewin’s honeyeater. Means with different letters are significantly different ($P < 0.05$ in LSD comparisons); see also Tables 2 and 3.

significant summer increases, consistent with immigration into the study region. The black-faced cuckoo-shrike, silvereve, little wattlebird, and pied currawong were recorded in substantially higher numbers during winter than summer. Numbers of the Lewin’s honeyeater and Torresian crow also differed between seasons, but their seasonal abundance turnover was less than 50%, and was probably due to factors such as reproduction or local movements rather than larger-scale migration. The remaining 18 species showed no significant difference in abundance between seasons. The decreasing response pattern detected for the rose-crowned fruit-dove was significant only during summer (Table 2). During winter,

numbers of this species were similar across site types, although its abundance was very low. The significant interaction detected in the ANOVA for the scarlet honeyeater was not supported by LSD tests, although a tendency towards a decreasing response pattern was shown in summer, with a trend towards an increasing response pattern in winter (Table 2).

The numbers of frugivorous birds (data for all species pooled) and of the wompoo and rose-crowned fruit-doves, white-headed and topknot pigeons and the brown cuckoo-dove in extensive forest at different elevations in summer and winter is shown in Table 4. We did not detect any significant ($P < 0.05$) interactions between the two factors using ANOVA, indicating that our data on bird abundance patterns were not strongly influenced by altitudinal movements of rainforest pigeons. Note that the superb fruit-dove was not recorded at any extensive forest sites in winter (Table 2).

Discussion

Frugivorous bird species vary in their response to landscape context and condition of rainforest patches

We treated extensive forest sites as a reference against which to quantify responses of frugivorous birds to forest fragmentation. Since remnants and extensive forest sites were similar in fleshy-fruited plant species composition, differences in frugivorous bird numbers between these two site types were most likely due to differences in site context rather than resource availability within the site. Differences in frugivorous bird numbers between remnant and extensive forests may reflect a response to several factors associated with the differing landscape context, including reduced total area of habitat, edge effects, or greater functional isolation. The patterns of bird abundance in regrowth sites reflect differences in both the availability of fleshy fruit resources and the landscape context.

Table 4. Frugivorous bird abundance pattern in high, mid- and low elevation sites during summer and winter. The mean (and standard error) number of individuals of all frugivores and selected rainforest pigeons is shown for each season (data from two surveys summed) in each elevation category; ANOVA P shows results of two-way ANOVA (E=elevation, S=season and ExS=interaction).

Bird species	Season	Elevation category (m a.s.l.)			ANOVA P		
		>500 (N=5)	200-500 (N=6)	<200 (N=5)	E	S	ExS
all frugivores	s	30.20 (4.24)	23.33 (1.92)	20.80 (2.85)	0.68	0.40	0.39
	w	20.80 (3.20)	21.17 (5.35)	23.40 (5.85)			
white-headed pigeon	s	0.00	0.83 (0.39)	0.20 (0.20)	0.29	0.39	0.14
	w	0.40 (0.41)	0.17 (0.16)	0.00			
wompoo fruit-dove	s	4.00 (0.96)	2.00 (0.57)	2.00 (0.85)	0.24	0.98	0.48
	w	3.00 (1.44)	1.67 (0.74)	3.40 (1.31)			
rose-crowned fruit-dove	s	2.00 (0.56)	3.50 (0.75)	2.80 (1.22)	0.51	0.0007	0.35
	w	0.40 (0.25)	0.17 (0.16)	1.20 (0.81)			
brown cuckoo-dove	s	3.40 (0.76)	2.83 (0.30)	2.00 (0.64)	0.15	0.16	0.56
	w	2.00 (0.85)	2.67 (0.33)	1.40 (0.61)			

A number of studies in different parts of the world have documented bird declines and local extinctions in fragmented rainforest (Johns 1991; Estrada *et al.* 1993; Kattan *et al.* 1994; Christensen and Pitter 1997; Restrepo *et al.* 1997; Warburton 1997; Renjifo 1999; Silva and Tabarelli 2000). The present study showed that the frugivorous bird species of the south-east Queensland region varied in their responses to rainforest fragmentation and regrowth; some responded negatively and others positively. Some species showed a different abundance response in remnant forest compared with that in rainforest regrowth. Other species showed no clear differences in abundance between extensive forest, remnants and rainforest regrowth.

Consistent with anecdotal evidence in Frith (1952), the wompoo, rose-crowned and superb fruit-doves were generally less abundant in remnants and regrowth than extensive forest. Despite being known to fly across cleared land (Frith 1952; Howe *et al.* 1981; Date *et al.* 1991), fruit-doves used remnant and regrowth rainforest habitats in the Sunshine Coast much less frequently than extensive forest areas. These three decreaser species are specialised frugivores, and similar patterns of declining numbers following forest disturbance have been reported elsewhere for other diet-specialist bird species (Kattan *et al.* 1994; Christensen and Pitter 1997; Restrepo *et al.* 1997). Fruit-doves are selective in terms of the range of plant species they consume (Crome 1975; Innis 1989) and the plants that characterise their diets are typically more common in well-developed than in regrowth rainforest (Crome 1990). The much lower numbers of fruit-doves in regrowth than in remnant or extensive rainforest may reflect the absence or very low availability of suitable food resources among pioneer vegetation. However, although a similar range of fleshy-fruited plant resources was available across our remnant and extensive forest sites, fruit-dove numbers were generally much lower in remnants. Although fruit-doves undertake regular movements through forest areas to accommodate the shifting availability of fruit resources (Innis 1989; Date *et al.* 1991; Price *et al.* 1999), the landscapes in which remnant sites are located may generally contain insufficient densities of fruiting plants to satisfy the energetic requirements of these fruit-specialists. Certainly, the abundance of a species within a forest patch can be influenced by that species' ability to use food and other resources from the surrounding area (Saunders *et al.* 1991; Fahrig and Merriam 1994; Price *et al.* 1999).

We detected the greatest changes in frugivore species numbers between regrowth patches and both the remnants and extensive forest areas, pointing to a greater effect of floristic and associated structural changes than interrupted forest cover *per se*. The brown cuckoo-dove and green catbird showed much lower abundance in regrowth than in remnants and extensive forest. Brown cuckoo-doves grind ingested seeds (Frith 1982), therefore deriving nutrition from seeds as well as fruit pulp. Birds with seed-grinding digestion may therefore be less restricted in their sources of energy than non-grinding fruit-specialists, which rely on the nutritional quality of the fruit pulp. This may explain why brown cuckoo-doves did not show the sensitivity to landscape context that fruit-doves did, and were recorded in similar numbers in remnant and extensive forest sites. Similarly, green catbirds eat a wide range of fruits (Innis

and McEvoy 1992) as well as flowers, invertebrates, and the eggs and nestlings of other birds (Blakers *et al.* 1984), and are therefore not as constrained as fruit-doves in their sources of nutrition. Although the brown cuckoo-dove is a fruit-specialist, its diet includes fruit from a range of plants that are common in rainforest regrowth and is noted for its conspicuousness in regrowth vegetation at forest edges (Frith 1952; Crome 1975). However, this species roosts in well-developed forest (Frith 1982) and is therefore unlikely to use regrowth that is distanced from developed forest. Furthermore, the brown cuckoo-dove (Frith 1982; Date *et al.* 1996) and green catbird (Innis and McEvoy 1992) are considered to be sedentary or only locally nomadic in subtropical rainforests (Blakers *et al.* 1984), and therefore possibly require a larger area of contiguous vegetation than is provided by most regrowth patches surveyed in this study. Overall, these areas were typically narrow strips or very small patches with low amounts of surrounding forest cover compared with remnant sites. Our data for these species may indicate area-sensitivity at very small patch sizes.

As well as decreaseers, the present study detected several species that increased in abundance in remnant and regrowth rainforest compared with extensive forest. Consistent with observations made during the 1950s in rainforest remnants in northern New South Wales (Frith 1952), the seed-grinding bar-shouldered dove was absent from extensive forest but invaded some rainforest remnant and regrowth patches. This may reflect greater availability of grasses or other food within and surrounding remnants and regrowth patches (Frith 1952).

Black-faced cuckoo-shrikes, figbirds, rainbow lorikeets, Torresian crows and silvereyes were found in similar abundance in fragmented and unfragmented rainforest but were higher in abundance in regrowth habitat. These species commonly use non-rainforest habitats (Blakers *et al.* 1984; Catterall *et al.* 1998), contrasting with the rainforest-dependent decreaseers. With the exception of the highly-frugivorous figbird, the increaseer birds in this study regularly eat a variety of food types, including a range of fleshy fruits (Blakers *et al.* 1984). As suggested earlier for the bar-shouldered dove, high numbers of these species in regrowth may reflect use of the types of resources occurring within and surrounding regrowth patches. For example, a high abundance of invasive fleshy-fruited exotic tree and shrub species ("fleshy-fruited weeds") including camphor laurel, large- and small-leaved privet and lantana, would boost the availability of food at various times in regrowth rainforests for opportunistic frugivores that may not be as selective as fruit-specialists.

Fleshy-fruited weeds, in particular camphor laurel, have been identified as potentially important food sources for the topknot and white-headed pigeons (Frith 1982; Innis 1989; Date *et al.* 1996). In fact, the apparent recovery of white-headed pigeon numbers throughout northern New South Wales since the early 1900s has been attributed firstly to the prohibition of hunting and secondly to the spread of camphor laurel (Frith 1982). Observations made from the 1920s suggested declining numbers of topknot pigeons following rainforest clearing (Frith 1952, 1982), and it has subsequently been proposed that camphor laurel fruits support remaining populations in the contemporary

landscape (Date *et al.* 1996). Unlike the fruit-doves, neither of these fruit-specialist species showed significantly different numbers in rainforest remnants or regrowth compared with extensive forests in the present study, although topknot pigeon numbers showed a decreasing trend. Further systematic sampling would be required to gain better understanding of how topknot pigeons use the contemporary landscape. White-headed pigeons are seed grinders (Frith 1982), deriving some nutrition from seeds and, as proposed earlier for the brown cuckoo-dove, may therefore be less constrained than non-grinding fruit-specialists by fruit pulp quality. It is also noteworthy that camphor laurel and privets usually bear fruit in winter, a time when the black-faced cuckoo-shrike (increaser), silvereye (increaser) and pied currawong (tolerant) are abundant in rainforests, and using these disturbed areas.

Seasonal changes in fruit-eating bird abundance

A greater abundance and diversity of native fleshy fruits are generally available in subtropical Australian rainforests during summer than during winter, while the opposite generally holds for the introduced weedy species (Innis 1989). This difference in fruit availability may influence the abundance of frugivorous birds in rainforest habitats within the study region. The common koel, channel-billed cuckoo, superb and rose-crowned fruit-doves increased substantially in numbers at the study sites during summer and all are common summer immigrants to the study region. The first two species are total migrants (Higgins 1999), and the two fruit-doves are considered to be partial migrants, with some individuals over-wintering in forests within the study region while the majority of the population appears to return to tropical forests in northern Australia or Papua New Guinea (Blakers *et al.* 1984). These species showed both decreasing (the fruit-doves) and tolerant (common koel and channel-billed cuckoo) response patterns in the present study.

The little wattlebird, black-faced cuckoo-shrike, pied currawong and silvereye increased substantially in numbers at the study sites during winter. The higher winter numbers of silvereyes reflect an influx of individuals of this species from the south to the study region (Blakers *et al.* 1984). The silvereye and the black-faced cuckoo-shrike were classed as increasers in the present study, while the other two winter-abundant species (little wattlebird and pied currawong) were classified as tolerant. All four species make use of remnant and especially regrowth rainforests, and their increased winter abundance may indicate a response to winter fruit availability in regrowth habitat, potentially including the winter-fruiting weeds. Indeed, silvereyes of a subtropical island population were found to increase their intake of fruit during winter (Catterall 1985), and pied currawongs have been reported to move from eucalypt open forests into rainforest during winter (Lindsey 1995), concurrent with a dietary shift from mostly stick insects to more fruit (Blakers *et al.* 1984). There is some evidence of a winter influx of the little wattlebird into eastern Queensland (Blakers *et al.* 1984). This species usually occupies coastal eucalypt forests and heathlands rather than rainforests (Blakers *et al.* 1984), and we recorded it mostly in coastal remnant and regrowth sites, possibly reflecting increased fruit intake during winter.

Date *et al.* (1991, 1996) suggested that there is seasonal altitudinal migration in some species of rainforest pigeons, with the general scenario of movement into upland forests during summer and lowland forests during winter. Our surveys may not have been conducted sufficiently frequently to detect such seasonal movement patterns. Nevertheless, our data do not show a substantial seasonal exchange of frugivorous bird numbers between extensive forest sites located at different elevations.

Frugivorous birds and seed dispersal in remnant and regrowth rainforest: conservation implications

The wompoo fruit-dove suffered population declines and localised extinctions from southern parts of its range (southern New South Wales) during the early part of the 20th century (Recher *et al.* 1995) and appeared to be declining in northern New South Wales from the late 1920s, following widespread rainforest clearing and fragmentation. Frith (1952) predicted that this species was "...doomed to early extinction..." (pp.91-92). Frith (1952) also forecast ongoing decline in superb fruit-dove populations as a result of rainforest loss but suggested the nomadic behaviour of rose-crowned fruit-doves would give them greater resilience to habitat destruction and fragmentation (Frith 1982). In contrast to recent observations in northern New South Wales (Gosper and Holmes 2002), the data presented in our study suggest that fragmented remnants and regrowth rainforest patches do not provide suitable habitat for significant numbers of these three bird species.

Dire consequences of frugivore declines have been predicted; based on investigations into plant recruitment without dispersal away from parents, Chapman and Chapman (1995) calculated that 60% of native plant species could be lost from forest fragments in Africa should frugivores disappear from these landscapes. While we classified a group of decreaser frugivores, we detected the replacement of these species by a group of increaser species. Increasers also potentially disperse rainforest seeds, but it is unclear whether these species move the same seeds as birds from the decreaser group. Silva and Tabarelli (2000) suggested that the loss of a subset of the frugivorous fauna (large-gaped frugivores) through hunting and habitat destruction in Brazilian rainforests may lead to the extinction of up to one-third of the native plant species of those forests. In south-east Queensland, the fruit-doves swallow larger fruits and seeds than most other frugivorous birds (Green 1993), by virtue of their distensible gapes (Frith 1982). The increaser figbird, however, may also be able to swallow large seeds. If increaser species do not disperse the same suite of large-seeded plants as the decreasees, fewer seedlings of such plants (possibly species from the Lauraceae, Elaeocarpaceae and Sapotaceae families) will be recruited to many rainforest regrowth or remnant patches. Our results indicate that larger-seeded plants may become less abundant in fragmented forests and be poorly represented among recruits to regenerating areas of south-east Queensland. Direct seeding or replanting of these species may be needed to maintain their representation in fragmented landscapes. Higher-order interactions involving fauna other than birds

also change in fragmented compared with extensively-forested landscapes (Turner 1996). Depending on the specific dispersal, predation or caching role of affected fauna species, changes to forest regeneration resulting from altered avian dispersal may be exacerbated or offset (Harrington *et al.* 1997; Wright *et al.* 2002).

The seeds of plants dispersed by increaser birds are likely to be moved into and around fragmented forests, particularly regrowth, at greater rates than in extensive forests. It has been suggested that fruits consumed by mixed diet, opportunistic frugivores, such as characterise the increaser species of the present study, are mostly sugary, watery and small-seeded (McKey 1975). Many fleshy-fruited weeds fit this description (Richardson *et al.* 2000) and their increased dispersal and recruitment in remnants and regrowth can be expected as a result of the regular use of these habitats by the increaser bird species. This may lead to positive feedback cycles between the fleshy-fruited weeds and the fragmentation-tolerant opportunistic frugivores in regrowth areas of highly disturbed rainforest landscapes.

Qualitative aspects of seed dispersal may also change in fragmented forests. For example, the abundance of two seed-grinding species increased (bar-shouldered dove and rainbow lorikeet), while only one (the brown cuckoo-dove) decreased in fragmented forest habitats. This may mean that a greater proportion of the seeds of fruits

eaten by these species are ground and destroyed than are dispersed in viable condition in fragmented compared with extensive forests, although neither of the increaser species seem to consume large amounts of fleshy fruit. Furthermore, features such as lump-lined stomachs are peculiar to the decliner fruit-doves (Crome 1975) and may provide different seed treatment and greater germination success compared with the digestive processes of other birds. Behavioural differences between frugivore species may also change finer-scale seed dispersal patterns (for example, seed shadows) in fragmented landscapes (Silva *et al.* 1996; Fuentes 2000).

Many frugivorous bird species were tolerant of changes associated with rainforest habitats in the fragmented study landscape, while the numbers of other frugivorous bird species increased in response to these changes. However, the birds we identified as decreaseers are not adequately conserved in the fragmented rainforests of south-east Queensland and we expect ongoing population declines if there is further clearing of rainforest. If these decreaseer species feed on a different suite of plants from those eaten by tolerant and, especially, increaseers, rainforest seed dispersal and forest regeneration will also vary between forested and fragmented landscapes. There is a potential for the decline or disappearance over time of certain plant species from remnant forests, arrested succession in regrowth areas, and increased abundance of introduced flora.

Acknowledgements

Cath Moran was supported during this project by a Commonwealth postgraduate award. Research funding was provided by the Rainforest Cooperative Research Centre (CRC). Many of the sites used in this study were located on private or Council-owned land and these landholders and custodians are gratefully acknowledged for their support. Many thanks to Dave Curmi for help in establishing the study plots and to Rachel King and Scott

Piper for discussion and advice relating to data analyses. Discussion with other members of the Wildlife Ecology Discussion Group at Griffith University, in particular Terry Reis and John Kanowski, are appreciated. Nick Clancy contributed thoughtful comments on the project and drafts of this manuscript. We are grateful to Aubrey Chandica for preparing the study site map. Two anonymous referees and Dan Lunney provided suggestions that improved the paper.

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APPENDIX I



The figbird is a frugivore which occurs in a very wide range of habitats, increasing in numbers from intact rainforest to fragmented regrowth ("increaser"). It is probably one of the major species capable of moving larger-seeded plants in highly-cleared landscapes. It is also a disperser of woody weeds.

Photos: Terry Reis



The superb fruit-dove is a rainforest-dependent bird that is rarely seen in remnant and regrowth patches ("decreaser"). It eats the fruits of rainforest plants, and is a disperser of their seeds.

Photos: Terry Reis