

1 **Title:** Reduced dispersal of native plant species as a consequence of the reduced
2 abundance of frugivore species in fragmented rainforest

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18 **Abstract**

19 Frugivorous animals disperse the seeds of the majority of rainforest plant species and
20 hence play a key role in the trajectory of rainforest regeneration. This study
21 investigated whether changes in the species composition of the frugivore community
22 in fragmented rainforest in subtropical Australia is likely to impact the dispersal of
23 native plant species. The potential of frugivorous bird and bat species to disperse the
24 seeds of plant species in fragmented rainforest was assessed using published dietary
25 information together with field surveys of their abundance within intact forest, forest
26 fragments and patches of regrowth. Frugivore species with reduced abundance in
27 fragmented rainforest were the only known dispersers of 27 of the 221 native plant
28 species in the data set (12% of species). These frugivore species were also major
29 dispersers of plant species producing fruits wider than 10 mm and species from the
30 families Rubiaceae, Lauraceae, Myrtaceae, Meliaceae, Lamiaceae and Vitaceae.
31 Except for Rubiaceae, these plant taxa are also potentially dispersed by two of the
32 frugivore species that were widespread in fragmented rainforest, *Lopholaimus*
33 *antarcticus* and *Ptilonorhynchus violaceus*, although dispersal rates are likely to be
34 lower in fragmented than in extensive rainforest. Consistent with other regions, large-
35 seeded plants are susceptible to reduced dispersal in fragmented rainforest in
36 subtropical Australia. However, we predict a smaller deficit in seed dispersal in
37 fragmented forests than has been reported from other regions, due to factors such as
38 functional overlap among frugivore species, the ability of many Australian rainforest
39 vertebrates to persist in fragmented rainforest, and a lack of hunting in these forests.
40 Nevertheless, rainforest fragmentation has reduced the abundance of a suite of
41 frugivorous rainforest fauna, which in turn is likely to reduce the dispersal of a certain

42 plant taxa and may alter patterns of plant regeneration in subtropical Australian
43 rainforest fragments.
44
45 **Keywords:** forest regeneration, restoration, seed dispersal, frugivory, ecosystem
46 function, secondary effect

47 **Introduction**

48 Throughout the world, rainforest clearing and fragmentation have resulted in
49 decreased populations of many frugivore species (Corlett, 1998; Renjifo, 1999;
50 Castelletta et al., 2000; da Silva and Tabarelli 2000; Cordeiro and Howe, 2001, 2003).
51 This may lead to reduced or failed dispersal of many plant species, because over 70%
52 of tree, shrub and vine species in tropical and subtropical rainforests produce seeds
53 enclosed in fleshy fruit that are dispersed by frugivorous vertebrates (Howe and
54 Smallwood, 1982; Willson et al., 1989). In particular, it has been predicted that large-
55 seeded plant species are unlikely to be dispersed in many fragmented tropical
56 rainforest regions as a result of widespread declines in the suite of frugivore species
57 that are capable of dispersing large seeds (Corlett, 1998, 2002; da Silva and Tabarelli,
58 2000; Kitamura et al., 2002; McConkey and Drake, 2002). In turn, reduced seed
59 dispersal may lead to lower rates of plant recruitment (Bleher and Böhning-Gaese,
60 2001; Cordeiro and Howe, 2003), increased vulnerability of plant populations to
61 localised extinction (Fahrig and Merriam, 1994), and limited potential for plant
62 colonisation of regrowth and restoration sites on previously- cleared land (Duncan
63 and Chapman, 2002; Kanowski et al., 2008).

64
65 However, there may be cases where the dispersal of plant species are resilient to
66 changes in the composition of the frugivore assemblage in fragmented rainforest.
67 First, most fleshy-fruited plant species appear to be dispersed by multiple frugivore
68 species (Wheelwright and Orians, 1982; Brown and Hopkins, 2002; Silva et al.,
69 2002). Second, some frugivore species usually persist in fragmented landscapes or
70 colonise these landscapes from other habitat types (Corlett, 1998; Renjifo, 1999;

71 Moran et al., 2004a). Hence, the decline of any particular frugivore species could
72 potentially be offset by other, functionally similar frugivore species.

73

74 Frugivorous birds and bats are the main seed dispersers in Australian subtropical
75 rainforests (Green, 1995), where 42 bird species and five bat species are at least partly
76 frugivorous (Moran et al., 2004a; Moran, 2007). Moran et al. (2004a) identified a
77 suite of frugivorous bird species, predominantly *Ptilinopus* spp., that was much less
78 abundant in fragmented than extensive rainforest in this region. Moran (2007) showed
79 that among frugivorous bats, one species (*Nyctimene robinsonii*) was less frequent in
80 rainforest regrowth than in remnant or extensive rainforest, whereas *Pteropus* spp.
81 were found in extensive, remnant and regrowth rainforest in the region.

82

83 This study aims to evaluate whether the low abundance of some frugivorous bird and
84 bat species in fragmented rainforest is likely to lead to the reduced dispersal of certain
85 plant taxa or whether these plants could potentially be dispersed by the frugivore
86 species that persist in fragmented rainforest. This work uses quantitative information
87 on the diets of frugivorous bird and bat species, together with data on their abundance
88 in fragmented rainforest, to assess the potential for reduced seed dispersal in
89 fragmented rainforest in subtropical Australia. A frugivore species' potential to
90 disperse seeds is assessed in terms of plant species, genus and family and fruit size.
91 Comparisons are made among individual frugivore species and among groups of
92 frugivores that showed different responses to fragmentation. We assert that the initial
93 difference between frugivore species in terms of their roles in seed dispersal is
94 whether or not they consume and potentially disperse viable seeds from a plant

95 species. This study is focused on whether a frugivore consumes and passes intact
96 seed, and does not consider subsequent variation in frugivore behaviour, which
97 determines the timing of dispersal, volume of seeds dispersed and spatial patterns of
98 seed deposition (Schupp, 1993). Following seed dispersal, factors that influence seed
99 germination, seedling survival and growth become important in terms of patterns of
100 plant recruitment away from parent plants (Wang and Smith, 2002; Clark et al.,
101 2007), but are not relevant if seed dispersal has failed.

102

103 The community-level approach used in this study is novel; previous studies of
104 frugivore species' roles in seed dispersal have generally been limited to a subset of the
105 frugivore and/or plant taxa comprising regional assemblages, and have been
106 especially concerned with large frugivores and large-fruited plants (e.g., Kitamura et
107 al., 2002; McConkey and Drake, 2002; Silva et al., 2002; although see Dennis and
108 Westcott, 2006).

109

110 **Methods**

111 *The study region and site network*

112 The study was conducted in a 4 000 km² subtropical rainforest landscape in the region
113 known as the Sunshine Coast, approximately 100 km north of the city of Brisbane in
114 southeast Queensland, Australia (approximately 26° - 27° S 152° - 153° E).

115 Continuous subtropical rainforest previously occurred on fertile soil on basalt lava
116 flows in the area (e.g., the Maleny plateau), and in areas of less fertile soils that
117 receive high rainfall, are locally nutrient-enriched and moist (e.g., along
118 watercourses), or are associated with topographic features that provide protection

119 from fire (e.g., gullies) (Webb and Tracey, 1981). Extensive areas of subtropical
120 rainforest have been cleared in Australia, especially from basalt plateaux, in the
121 lowlands and along watercourses, with large forest tracts now mostly restricted to
122 steeper slopes (Webb and Tracey, 1981). Contemporary rainforest landscapes in
123 Australia resemble those in many other regions of the world in comprising a mosaic
124 of remnant forest patches, grazed land, agricultural cropland, tree crops, regrowth and
125 urban development, interspersed with small areas of rainforest restoration.

126

127 Study sites were chosen to represent three states of rainforest context and condition in
128 which rainforest remained or had re-established in the Sunshine Coast region. Sixteen
129 replicate sites within each of three different states of rainforest landscape context
130 (fragmented or continuous) and condition (remnant or regrowth) were selected: (i)
131 rainforest within extensive tracts of forest; (ii) remnant rainforest isolated from
132 extensive forest by surrounding cleared and modified land; and (iii) regrowth, also
133 isolated from other rainforest (n = 48). Remnant forest sites were chosen to have
134 similar floristic and structural attributes to extensive forest, although remnant sites
135 tended to have more native pioneer and exotic plant species and a simpler forest
136 structure than extensive forest, especially near edges. The sizes of remnant sites
137 ranged from 2 ha - 100 ha (mean 46.1 (s.e. 9.4) ha). Regrowth sites had been
138 regenerating for at least 10 – 20 years, mostly on former grazing land. Regrowth sites
139 had developed a tree layer, approximately 10 –15 m in height, but lacked the
140 abundance and diversity of large diameter trunks that were present in remnant and
141 extensive forest sites. Regrowth sites were 2 – 10 ha in size (mean 3.4 (s.e. 0.5) ha).
142 Sites of the same type were separated by at least 2 km, and most were more than 5 km

143 apart. Sites of different types were also usually well separated. Most remnant and
144 regrowth sites were 5-10 km from extensive forest, although some sites were located
145 further away. Many of the study sites (34 of 48) were located near a watercourse. The
146 abundance of 42 frugivorous bird species and distribution of three frugivorous bat
147 species were surveyed in this network of 48 sites.

148

149 *Frugivorous bird and bat species' abundances and fragmentation response patterns*

150 The patterns of abundance of 42 frugivorous bird species were determined from 40
151 minute searches of a 1 ha plot at each site, conducted twice in summer and twice in
152 winter, during 2001 by CM (described in detail in Moran et al., 2004a). Of the 26 bird
153 species that were recorded frequently enough to assign a fragmentation response
154 pattern (i.e., detected in at least five of the 48 sites during either summer or winter
155 surveys), nine are known to destroy seeds (i.e., 'seed crushers'; see Moran et al.,
156 2004b) and are not considered further in this paper as they probably disperse few
157 viable seeds compared with non-seed crushing frugivore species. One additional
158 species (*Myzomela sanguinolenta*) was also excluded from analyses presented here
159 due to the low number of observations of fruit consumption that had been recorded at
160 the level of plant species. Therefore, 16 frugivorous bird species are considered in this
161 study.

162

163 The occurrence of three species of foraging frugivorous bats (*Pteropus poliocephalus*,
164 *P. alecto* and *Nyctimene robinsonii*) was assessed using a single, hour-long nocturnal
165 search along a 400-500 m trajectory at each site during summer (January-February)
166 2003 (described in Moran, 2007). Surveys were timed to occur during the period of

167 maximum fruit abundance in rainforest in subtropical Australia (Innis, 1989; Church,
168 1997). Presence-absence data were used as the quantitative measure of site use for
169 frugivorous bat species. Because it was often not possible to distinguish between the
170 two *Pteropus* species, data for were combined in analyses (*Pteropus* spp.). Two
171 additional frugivorous bat species (*P. scapulatus* and *Syconycteris australis*) were
172 recorded only once during surveys and are not considered further.

173

174 Earlier work has detailed the results of surveys of the abundance and distribution of
175 frugivorous bird and bat species in the site network (Moran et al., 2004a, b; Moran,
176 2007). In summary, based on statistical comparisons of their abundance using
177 Analysis of Variance (ANOVA), frugivore species were classified as showing one of
178 three patterns of abundance in remnants and regrowth, relative to extensive forest: (i)
179 lower numbers in remnant and/or regrowth rainforest patches compared with
180 extensive forest ('decreaser' pattern, four bird species and one bat species); (ii) higher
181 numbers in remnant and/or regrowth rainforest patches compared with extensive
182 forest ('increaser' pattern, five bird species); or (iii), no clear difference in numbers
183 between the three site types ('tolerant' pattern, seven bird species and *Pteropus* spp.)
184 (Moran et al., 2004a; Moran, 2007). Because of their absence or low abundance in
185 fragmented rainforest, frugivore species that showed the decreaser response have a
186 relatively low potential to disperse seeds in these areas. Species showing the tolerant
187 or increaser response patterns potentially disperse seeds in fragmented rainforest.
188 Frugivore species were grouped by their abundance pattern ('fragmentation response
189 groups') for some statistical analyses.

190

191 *Patterns of fruit consumption by frugivore species*

192 Information about the fleshy-fruited plant species consumed was collected for the 16
193 frugivorous bird species, *N. robinsonii*, *P. poliocephalus* and *P. alecto*. Data for the
194 two *Pteropus* spp. were combined in analyses to be consistent with the treatment of
195 abundance data and because there is substantial overlap in the diets of these species
196 (Eby, 2006). *Pteropus* spp. are henceforth treated as a single species in analyses and
197 discussion. Dietary data were obtained from 107 published sources (contained in
198 Appendices of Moran, 2007) and several unpublished data sets (see
199 Acknowledgements). Most of the feeding records were based on direct field
200 observation although a small number were obtained from gut contents, scats, or
201 regurgitated seeds. For a given frugivore species, the data potentially included
202 foraging records from multiple years, seasons and geographic locations. There was
203 large variation among frugivore species in the amount of foraging information
204 available. Because of the wide geographical range of many of the frugivore species
205 that occur in subtropical Australia, feeding records may have been collected from an
206 area extending from temperate southern Australia to tropical Papua New Guinea.
207 Plant species that are introduced to Australia from other countries, or that are native to
208 other regions of Australia but do not naturally occur in subtropical Australia, were
209 considered to be exotic plant species (native and exotic plant taxa are shown in the
210 Appendices of Moran (2007)). Three data sets were compiled from this information:
211 i) a binary matrix showing whether or not each fleshy-fruited plant species had been
212 recorded in the diet of each of the frugivore species; ii) the number of native plant
213 species from each genus that had been recorded in the diet of each frugivore species;
214 and iii) the number of native plant species from each family that had been recorded in

215 the diet of each frugivore. This information was considered to reflect the potential of
216 each frugivore species to disperse the seeds of each plant taxon.

217

218 Dietary data were also used to examine frugivore species' patterns of fruit size
219 consumption. The measure of fruit size used in this work was the width of the
220 minimum dispersal unit ('the diaspore', van der Pijl, 1982). For most plant species,
221 this was the shorter axis (usually diameter) of the whole fruit. However, because
222 piecemeal consumption of soft fruits with small seeds (e.g., many species in the
223 Moraceae or Solanaceae) and dehiscent arillate fruits (e.g., many species in the family
224 Sapindaceae), may result in the dispersal of viable seed (Corlett, 1998; Kitamura et
225 al., 2002), the size of the diaspore for these plant species was taken as the width of the
226 seed or the width of the seed plus the fleshy aril, respectively. Diaspore size data were
227 collected from literature (Williams et al., 1984; Floyd, 1989; Cooper and Cooper,
228 1994; Hauser and Blok, 1998; Butler, 2003), supplemented with data from field
229 collections (S. McKenna, C. Moran) and biological web sites. In most cases, a range
230 of diaspore size values was reported and the median of these was used in analyses.

231

232 Diaspore size information was also used to exclude likely instances of fruit theft by
233 birds (i.e., consumption of the fruit flesh without dispersal of the seed (Howe and
234 Estabrook, 1977)) from reported feeding records. Because the size of fruit that a bird
235 can swallow is constrained by its gape width (Herrera, 1981; Wheelwright, 1985),
236 records were excluded from the data set if the median diaspore size was more than
237 twice the gape width of the bird species (Moran et al., 2004b). A small percentage

238 (approximately 5%) of records were excluded on this basis. This approach accounts
239 for the potential for substantial intraspecific variation in fruit size (Edwards, 2005).

240

241 *Data analyses*

242 *Comparison of dietary composition among frugivore species and fragmentation*

243 *response groups*

244 The number of native plant species, genera and families, the proportion of plant
245 species with a median diaspore size ≥ 10 mm, and the average diaspore size of plant
246 species consumed were calculated for each frugivore species. To examine similarities
247 among the frugivore species in terms of their dietary composition, a classification tree
248 was generated using the UPGMA algorithm (Manly, 1994) in PRIMER (5.2.9)
249 (Clarke and Warwick, 2001), with the Bray-Curtis similarity metric. Exotic plant
250 species and species that had been recorded in the diet of less than two frugivore
251 species were excluded from multivariate analyses. For analyses at higher taxonomic
252 levels, genera or families with only one plant species in the data set were excluded.
253 The bird species *Scythrops novaehollandiae*, *Gymnorhina tibicen* and *Anthochaera*
254 *chrysoptera* were not included in multivariate analyses because of the low number of
255 native plant species that had been recorded in their diets. Data for *N. robinsonii* were
256 not included in any statistical analyses of dietary patterns because of the small amount
257 of dietary information available for this species.

258

259 The statistical significance of overall dietary differences between frugivore species
260 that showed decreaser, tolerant and increaser patterns was tested using Analysis of
261 Similarity, with 9 999 iterations (ANOSIM; Clarke and Green, 1988), also in

262 PRIMER. ANOSIM tests for statistical differences among sampling units (e.g.,
263 fragmentation response groups) using Monte Carla randomisation to determine
264 whether the rank similarities within groups are greater than those between groups.
265 Spearman rank correlations were used to test for associations between the
266 susceptibility of a frugivore species to decline in fragmented forest (scored as
267 increaser (low) = 1, tolerant = 2, decreaser (high) = 3) and the total number of native
268 plant species, genera and families that each consumed, as well as for the number of
269 native plant species consumed from each of the 13 plant families with at least five
270 species in the data set. The dietary proportions of exotic plant species and of native
271 plant species with large (≥ 10 mm diameter) diaspores were compared among
272 decreaser, tolerant and increaser frugivore species, also using Spearman's rank
273 correlations. The statistical test included a correction for multiple tied ranks.

274

275

276 The potential for functional substitution in fragmented rainforest by frugivore species
277 was quantified as the percentage of plant species in the diet of each decreaser
278 frugivore that was also consumed by each other frugivore species. The potential for
279 substitution for individual decreaser species by particular groupings of other frugivore
280 species was also quantified in this way.

281

282 The number of native plant species that would be without a known disperser if each
283 individual frugivore species was absent was calculated as the number of plant species
284 recorded solely in the diet of that frugivore species. The attributes of the plant species
285 that were recorded only in the diet of decreaser frugivores were identified in terms of

286 taxonomic affiliation at the family and genus levels, growth form and diaspore size.
287 The occurrence of these attributes among the plants only consumed by decrease
288 frugivores was compared with their frequency among remaining plant species in the
289 data set using chi-squared tests on cross-tabulations of plant species' frequencies
290 within attribute classes in SPSS (2001).

291

292 **Results**

293 *Dietary comparisons among frugivore species*

294 The diet data matrix comprised information for 221 native plant species from 146
295 genera and 62 families. An additional 33 plant species had been introduced to
296 subtropical eastern Australia from other continents, and three had been introduced
297 from tropical Australia (collectively referred to as “exotic species”). The data on the
298 occurrence of these plant species' in the diets of the 18 frugivore species yielded
299 records of 978 unique combinations of plant and frugivore species. Most of the native
300 (71%) and exotic (75%) plant species had been recorded in the diet of more than one
301 frugivore species.

302

303 There was considerable variation among frugivore species in the numbers of native
304 plant species they were known to consume, ranging from one (*G. tibicen*) to 106 (both
305 *Meliphaga lewinii* and *Ptilonorhynchus violaceus*; Table 1). This variation may
306 reflect differences among frugivore species in their diet breadth or level of frugivory,
307 as well as differences in sampling effort.

308

309 The plant species composition of the diets of three decreaser frugivore species
310 (*Ptilinopus magnificus*, *P. regina* and *Ailurioedus crassirostris*) were similar to one
311 another and were also similar to two tolerant bird species: *Lopholaimus antarcticus*
312 (which closely resembled the *Ptilinopus* species) and *P. violaceus* (similar to *A.*
313 *crassirostris*). The tolerant *M. lewinii*, *Strepera graculina*, *Pteropus* spp. and
314 increaser *Sphecotheres viridis* had the next most similar dietary composition to the
315 group containing these decreaser species (Figure 1). The superb fruit-dove's diet
316 comprised a subset of the other decreaser bird species, probably a reflection of it
317 being an uncommon summer migrant to the study region (Innes, 1989; Date et al.,
318 1996). ANOSIM showed that the overall native plant composition of the diets of four
319 decreaser frugivore species was statistically different from that of the four increaser
320 frugivores at the level of plant species (global $R = 0.264$, $p = 0.03$; pairwise
321 comparison between decreaseers and increaseers $p = 0.03$), genus (global $R = 0.188$, $p =$
322 0.06 ; pairwise $p = 0.03$) and family (global $R = 0.242$, $p = 0.04$; pairwise $p = 0.06$).

323

324 There was a positive association between a frugivore species' susceptibility to decline
325 in fragmented forest and the number of native plant species ($R_s = 0.45$, $p = 0.04$),
326 genera ($R_s = 0.46$, $p = 0.03$) and families ($R_s = 0.46$, $p = 0.03$) that they consumed
327 (Table 1) and the average dietary proportion of native plant species with large
328 diaspores (≥ 10 mm diameter) ($R_s = 0.67$, $p = 0.003$, Figure 2). There was substantial
329 variation among individual frugivore species within the tolerant response group, with
330 only two bird species (*L. antarcticus*, *P. violaceus*) and *Pteropus* spp. consuming
331 dietary proportions of native plants with large diaspores within the range shown by
332 decreaser birds (Figure 2). There was a negative association between a frugivore

333 species' susceptibility to decline in fragmented forest and the percentage of exotic
334 plant species in the diet, with exotic plant species comprising an average of 41% of
335 species in the diets of increaser frugivores, 17% of tolerant species' diets and only 8%
336 of decreaseers' diets ($R_s = -0.72$, $p = 0.001$).

337

338 Among the 13 plant families that had more than five species represented in the data
339 set, there was a positive association between a frugivore species' susceptibility to
340 decline in fragmented forest and the number of plant species consumed from
341 Lauraceae, Meliaceae, Myrtaceae, Rubiaceae, Lamiaceae and Vitaceae (Table 2,
342 Figure 3). One or more of several tolerant frugivores (*L. antarcticus*, *P. violaceus*, *M.*
343 *lewinii*, *S. graculina* and *Pteropus* spp.) consumed numbers of plant species from all
344 of these families within the range shown by decreaseer species. The only increaser
345 frugivore known to consume comparable numbers of native plant species from any of
346 these families was *S. viridis*, which consumed numbers of species from Lauraceae and
347 Meliaceae within the range of decreaseer bird species (Figure 3).

348

349 *Specific substitution potential among frugivore species*

350 Among tolerant and increaser frugivores, two tolerant species, *L. antarcticus* and *P.*
351 *violaceus*, consumed the greatest percentage of plant species that were consumed by
352 individual decreaseer species (Table 3; 56-73% and 52-66% respectively). A moderate
353 percentage of the plant species recorded in the diets of individual decreaseer frugivore
354 species was consumed by the tolerant *M. lewinii* (38-49%), *S. graculina* (35-48%),
355 *Pteropus* spp. (27-36%) and increaser *S. viridis* (40-53%), while other non-decreaseer
356 frugivore species consumed only a small percentage of the plant species that had been

357 recorded in the diets of decreaseers (Table 3). In combination, *L. antarcticus* and *P.*
358 *violaceus* consumed 72-81% of the plants recorded in the diets of individual decreaseer
359 frugivore species. The cumulative effect of remaining tolerant frugivores increased
360 the percentage of shared plant species to 80-86%, while the addition of increaseer
361 species did not increase this further (80-88%) (Table 3).

362
363 Twenty-seven native plant species were recorded only in the diet of decreaseer bird
364 species. These plants varied widely in their taxonomy, growth form and diaspore size,
365 although plant species from the Rubiaceae comprised a much greater percentage of
366 the 27 species (26%), than they did in the remainder of the data set (2%) ($\chi^2 = 27.1$,
367 $p < 0.0001$). Tree species comprised a smaller percentage of plants consumed only by
368 decreaseer frugivores (29%), compared with the percentage of trees among the
369 remaining species in the data set (52%) ($\chi^2 = 4.02$, $p = 0.045$). Among the plant
370 species that were only known to be consumed by decreaseers, there was no significant
371 difference in the number of species that were shrubs (41% of the plants only
372 consumed by decreaseers, 33% of plants in the remainder of the dataset, $\chi^2 = 0.32$, $p =$
373 0.57), vines (29%, 15%, $\chi^2 = 2.93$, $p = 0.086$) had large (≥ 10 mm) diaspores (48%,
374 40%; $\chi^2 = 0.37$, $p = 0.54$). Eight of the 27 plant species that were only known to be
375 consumed by decreaseer frugivores belong to genera that were consumed by other (i.e.,
376 non-decreaseer) frugivore species, and all but one of the plant species (*Elaeagnus*
377 *triflora*, the only Australian representative of the family Elaeagnaceae) were from
378 families that were known to be consumed by non-decreaseer species.

379

380 Among non-decreaser birds, *M. lewinii*, *P. violaceus* and *S. viridis* were the unique
381 consumers of a relatively high number of native plant species (20, 12 and 8,
382 respectively, Table 1). Most other non-decreaser frugivore species had few native
383 plant species for which they were the only recorded consumer (Table 1). All of the
384 plant species that had been recorded in the diets of *Pteropus* spp. were known to be
385 consumed by at least one frugivorous bird species.

386

387 **Discussion**

388 *Reduced dispersal of native rainforest plants as a consequence of rainforest* 389 *fragmentation*

390 The reduced abundance of a small number of frugivore species in fragmented
391 rainforest in subtropical Australia is likely to have reduced the dispersal of a number
392 of native plant species in these parts of the landscape. Assessment of the functional
393 roles of frugivorous bird and bat species in seed dispersal indicates that 12% of native
394 rainforest plant species may lack a dispersal agent in fragmented rainforest. The
395 ecological process of seed dispersal appears to be more intact in fragmented
396 rainforests of subtropical Australia than in other heavily cleared regions of the world,
397 where it has been predicted that approximately one-third of native rainforest plants
398 may suffer failed dispersal as a consequence of frugivore declines (e.g., da Silva and
399 Tabarelli, 2000). The persistence of most frugivore species in fragmented rainforest in
400 subtropical Australia means that there is the potential for maintained seed dispersal of
401 many plant taxa. It has been proposed that Australian rainforest fauna may have a
402 relatively high resilience to anthropogenic fragmentation of rainforest, given that
403 extant species have persisted through the ‘natural fragmentation’ of rainforest

404 resulting from contractions to refugial sites during the Pleistocene (Corlett and
405 Primack, 2006). Furthermore, frugivores are rarely hunted in subtropical Australia,
406 whereas hunting is a ubiquitous feature of rainforests in other regions (Corlett, 1998,
407 2002; Hamman and Curio, 1999; McConkey and Drake, 2002; Terborgh and Nuñez-
408 Iturri, 2006).

409

410 While many plant species do regenerate despite reduced or even failed seed dispersal
411 (Janzen and Martin, 1982; Corlett and Turner, 1997), their recruits are likely to be less
412 abundant and more spatially aggregated, and populations are more vulnerable to
413 extinction, than in forest with an intact disperser assemblage (Bleher and Böhning-
414 Gaese, 2001; Cordeiro and Howe, 2003). These plant species would also have limited
415 potential to colonise secondary regrowth or restoration sites on previously cleared
416 land (Duncan and Chapman, 2002; Kanowski et al., 2008).

417

418 The plant family Rubiaceae appears to be particularly vulnerable to reduced dispersal
419 in fragmented rainforest landscapes of subtropical Australia. Low recruitment of
420 plants in the Rubiaceae has been shown in remnant rainforest patches in both Brazil
421 (Tabarelli et al., 1999) and Singapore (Turner et al., 1996), although this has been
422 attributed to unsuitable germination conditions for these plants in fragments. While
423 germination conditions play an important role in plant regeneration patterns, low
424 recruitment of plants from the Rubiaceae in fragments may also be a consequence of
425 reduced seed dispersal in fragmented forest. The pattern we document of only a small
426 number of potential dispersers of plants from the Rubiaceae in subtropical Australia
427 may also be a general pattern in other regions. Izhaki et al. (2002) found that

428 anthraquinone, which deter consumption by some bird species, were common in
429 species of Rubiaceae in Israel, indicating that fruit chemistry may play a role in
430 limiting the consumption of Rubiaceae to a small subset of frugivores.

431

432 Other plants that are likely to have suffered reduced dispersal in fragmented rainforest
433 in subtropical Australia include species that produce diaspores wider than 10 mm, or
434 from the families Lauraceae, Meliaceae, Myrtaceae, Lamiaceae and Vitaceae. A
435 susceptibility of Lauraceae, Myrtaceae and Meliaceae to reduced recruitment in
436 rainforest fragments has been identified other regions (Turner et al., 1996; Tabarelli et
437 al., 1999), where they are also only consumed by a subset of the frugivore assemblage
438 (Snow, 1981; da Silva and Tabarelli, 2000).

439

440 We predict that reduced seed dispersal of certain plant families will lead to reduced
441 recruitment of some plant taxa and ultimately to changed patterns of forest
442 regeneration in fragmented rainforest. These predictions depend on the assumption
443 that changes in factors that affect seedling establishment, such as microclimatic
444 conditions or the abundance and behaviour of seed and seedling predators, do not
445 overwhelm the influence of altered seed dispersal patterns (Clark et al., 2007).

446 Empirical data on plant recruitment could be used to test the predictions that there will
447 be reduced rates and increased spatial aggregation of recruitment of plants in
448 Lamiaceae, Lauraceae, Meliaceae, Myrtaceae, Rubiaceae, Vitaceae, and species with
449 diaspores ≥ 10 mm in fragmented rainforest (e.g., Neilan et al., 2006).

450

451 *Key substitute seed dispersers in fragmented forest*

452 Many native plant species are likely to retain the potential for seed dispersal in
453 fragmented rainforest of subtropical Australia. Although the frugivore species with
454 reduced abundance in fragmented parts of the landscape disperse a large number and
455 diversity of plant species, most of these are also probably dispersed by at least one
456 non-decreaser frugivore. However, dispersal rates of these plant species may still be
457 lower in fragmented rainforest, since substitute dispersers may not compensate for the
458 absence of decreaser frugivores by consuming higher quantities of fruits (Kirika et al.,
459 2008). Quantitative differences in the contributions of different plant species to
460 frugivores' diets (e.g., Poulsen et. al 2002) may increase the impacts of losing some
461 frugivores beyond any expectations based on the simple presence of plant species in
462 their diets. Furthermore, because different frugivore species may vary in their small-
463 scale patterns of habitat use, the absence or reduced abundance of one species may
464 have consequences for dispersal of seeds to certain microsites or over certain
465 distances (Spiegel and Nathan, 2007).

466

467 The two non-decreaser species with the greatest potential to substitute for decreasers
468 as seed dispersers in fragmented parts of the landscape are *L. antarcticus* and *P.*
469 *violaceus* . Other frugivore species that potentially substitute for decreaser frugivore
470 species as dispersers of some of the plant taxa identified in this work as being
471 susceptible to reduced dispersal in fragmented rainforest are *M. lewinii*, *S. graculina*,
472 *Pteropus* spp. and *S. viridis*. Among the frugivorous bird species whose diets were not
473 analysed in this study because they were very uncommon in field surveys, only
474 *Sericulus chrysocephalus* had a diet that was similar in terms of plant species

475 composition to decreaser species (Moran, 2007). In particular, *S. chrysocephalus* may
476 contribute to the dispersal of plants with large diaspores and from the families
477 Rubiaceae, Meliaceae, Myrtaceae, and Vitaceae, although it is uncertain whether or
478 not this species is likely to disperse seeds among fragmented rainforest patches.

479 Although frugivory and seed dispersal by possums (e.g., *Trichosurus vulpecular*) and
480 small rodents (e.g., *Rattus fuscipes*) are likely to be uncommon, they may disperse the
481 seeds of some native plant species at a local scale, although would probably destroy
482 most seeds.

483

484 Despite the potential for tolerant and increaser frugivores to disperse native plant
485 species, a large proportion of the seeds dispersed in fragmented rainforest may
486 actually be exotic plant species. Exotic plant species are ubiquitous in fragmented
487 parts of the landscape (Buckley et al., 2006) and the frugivore species that use
488 fragmented rainforest in subtropical Australia, particularly increaser bird species,
489 consume fruits from large numbers of exotic plant species.

490

491 This study assessed the potential of frugivore species to substitute for one another as
492 seed dispersers based on their dietary composition. The actual capacity of a frugivore
493 to disperse seeds within and between fragmented rainforest habitats is also influenced
494 by the spatial scale of its foraging and ranging behaviour, combined with its gut
495 passage rate (Schupp, 1993; Dennis and Westcott, 2006). Among the frugivore
496 species identified as key substitute seed dispersers in fragmented rainforest, *L.*
497 *antarcticus* and *S. viridis* regularly travel rapidly over many kilometres across cleared
498 land and consequently may disperse seeds among widely spaced rainforest patches

499 (Frith, 1957; Price et al., 1999; Dennis and Westcott, 2006; Neilan et al., 2006). The
500 short gut passage rate of *S. viridis* (Dennis and Westcott, 2006) may limit its potential
501 to transport seeds over long distances (e.g., kilometres). On the contrary, the slow
502 transit of seeds through the gut of *L. antarcticus* may mean that it disperses few seeds
503 over short distances (e.g., within a remnant patch). *Pteropus* spp. travel tens of
504 kilometres in a night and may disperse very small seeds (e.g., 1- 4 mm diameter) over
505 long distances (Eby, 1991; Shilton et al., 1999). *Pteropus* spp. may disperse
506 moderately-sized diaspores over tens of metres in their cheek pouches, whereas large
507 diaspores may only be transported a short distance away from parent plants in claws
508 (Eby, 1991, 1995). Of the remaining key substitute dispersers, both *P. violaceus* and
509 *M. lewinii* move slowly over short distances (Dennis and Westcott, 2006), and hence
510 may disperse relatively few seeds between isolated rainforest fragments.

511

512 In subtropical Australian rainforest, frugivorous bats have the potential to disperse
513 seeds from many of the plants that are dispersed by birds. Consistent with Eby (1998),
514 the present study has shown high dietary similarity among birds and bats in this
515 region. There is no suggestion of a ‘bat fruit syndrome’ (van der Pijl, 1982),
516 previously proposed on the basis of limited overlap between the diets of frugivorous
517 birds and certain pteropid (e.g., Hamann and Curio, 1999; Bollen et al., 2004;
518 Richards, 1990) or phyllostomid (e.g., Gorchov et al., 1995) bat species. Although
519 frugivorous bats do not disperse a different suite of plant species to frugivorous birds
520 in Australia, they may play an important role in the transport of seeds to treeless
521 areas, because they can defecate in flight, whereas birds tend to eliminate seeds while
522 perched.

523

524 *Implications for rainforest conservation and ecological restoration*

525 Because of changes in the composition of the frugivore assemblage, the regenerative
526 potential of a substantial proportion of native rainforest plant species is likely to have
527 been reduced in fragmented parts of subtropical Australia. Continued rainforest
528 clearing would probably exacerbate the situation for frugivore species whose numbers
529 are already low in fragmented rainforest, and may lead to population declines of
530 additional frugivore species, with ensuing reductions in the dispersal and regeneration
531 of native plant species.

532

533 Rainforest restoration that meets the needs of fragmentation-sensitive frugivore
534 species should also eventually restore the seed dispersal potential of plant species that
535 have suffered reduced dispersal as a consequence of frugivore declines. In the short-
536 term, the reduced regenerative capacity of these plant species means that forest
537 regeneration in rainforest remnants, regrowth or replanting sites will not proceed
538 along successional trajectories observed in intact forest systems (Kanowski et al.,
539 2008). Changes in the abundance of seed predators or herbivores in fragmented
540 rainforest will also affect the process of forest regeneration because of their influence
541 on patterns of seed survival and germination, and seedling growth (Clark et al., 2007).
542 It is recommended that rainforest restoration programs incorporate the direct
543 introduction, via planting or direct-seeding, of native plant species with diaspores
544 10mm and wider, and from the Rubiaceae, as well as Lauraceae, Meliaceae,
545 Myrtaceae, Lamiaceae to enhance the resilience of populations of these species in
546 fragmented forests and to enable their representation among regenerating forest on

547 previously-cleared land. Because of their potential to smother young plants, it is not
548 recommended that vines from the family Vitaceae be included in early stages of
549 restoration.

550

551 Developing our understanding of the factors that influence distribution patterns in
552 fragmented rainforest of key potential substitute dispersers is required because the
553 loss of these species would have a disproportionate effect over seed dispersal. For
554 example, *L. antarcticus* is widespread throughout fragmented subtropical rainforest in
555 some landscapes (Date et al., 1996; Gosper and Holmes, 2002; Neilan et al., 2006;
556 this study), but this species has previously undergone dramatic population declines
557 (Frith, 1952, 1957; Date et al., 1996), and has a restricted distribution in small
558 subtropical rainforest fragments (Howe et al., 1981). Similarly, numbers of *Pteropus*
559 spp. (especially *P. policephalus*) have declined drastically in subtropical Australia
560 (Eby and Lunney, 2002), as have pteropid populations throughout the Old World
561 tropics (Fujita and Tuttle, 1991). The abundance of *Ptilonorhynchus violaceus* may be
562 limited in certain parts of fragmented rainforest landscapes, for example in areas
563 dominated by weedy regrowth (Neilan et al., 2006). The distribution of this species
564 may also be related to the location of display sites ('bowers'), which may in turn be
565 associated with landscape topography (Crome and Moore, 1989). Populations of *M.*
566 *lewinii* appear to be stable (Blakers et al., 1984; Higgins et al., 2001), although
567 interspecific interactions in fragmented rainforest (e.g., with the aggressive noisy
568 miner *Manorina melanocephala* (Piper and Catterall, 2003)) may affect the
569 distribution of closely related *M. lewinii*. *S. viridis* appears to be ubiquitous in
570 fragmented rainforest throughout its range, including in weedy regrowth and

571 replanted rainforest (Crome et al., 1994; Neilan et al., 2006; this study), and
572 populations of *S. graculina* also appear to be increasing (Higgins et al., 2006).

573

574 This study has developed an approach to understanding the consequences of changes
575 in the species composition of a frugivore assemblage for the important ecosystem
576 function of seed dispersal. Despite a relatively high level of resilience to rainforest
577 fragmentation among the frugivore species in subtropical Australia, the dispersal of
578 12 % of native plant species may have been substantially reduced in fragmented
579 rainforest in this region. As a consequence, the plant species composition of
580 fragmented rainforest may diverge from that in extensive tracts of forest over time,
581 with follow-on effects for other rainforest biota and ecological processes.

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593

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805 **Table legends**

806

807 **Table 1** For each frugivore species, their frequency in field surveys, the number of
808 native and exotic plant species, and the number of species that bear diaspores with a
809 median width < 10 mm and ≥ 10 mm, consumed. The number of genera and families
810 represented among the native plant species consumed by each frugivore species are
811 shown. ‘Only known consumer’ shows the number of plant species for which there
812 was no other known consumer.

813

814 **Table 2** The average number of native plant species from selected families consumed
815 by decreaser ($n = 4$), tolerant ($n = 8$) and increaser ($n = 5$) species. The total number
816 of native plant species in the data set from each of these families is shown. Significant
817 ($p < 0.05$) results are shown in bold.

818

819 **Table 3** The percentages of native plant species that were recorded in the diets of
820 each decreaser bird species (column head) and also consumed by each other frugivore
821 (bird or bat) species (row head)¹, and by particular groups of species (‘Frugivore
822 groups’). The number of native plant species consumed by each frugivore species, and
823 the species codes used in this table are shown in Table 1.

824

825

826

Table 1

Response pattern ¹	Common name ²	Genus and species	Family	Frequency in surveys ⁴		Number of plant taxa						Only known consumer		
						Total number		Species			Genera		Families	
						Sites	Indivs	Native <10 mm	Native ≥10 mm	Exotic				
										<10 mm	≥10 mm		Total	
Decreaser	wompoo fruit-dove	<i>Ptilinopus magnificus</i>	Columbidae	25	120	34	47	81	4	0	4	50	31	6
	superb fruit-dove	<i>P. superbus</i>	Columbidae	13	15	13	13	26	3	1	4	19	14	1
	rose-crowned fruit-dove	<i>P. regina</i>	Columbidae	36	101	41	33	74	6	1	7	50	28	5
	green catbird	<i>Ailurioedus crassirostris</i>	Ptilonorhynchidae	35	148	60	44	104	7	0	7	75	38	8
	eastern tube-nosed bat	<i>Nyctimene robinsonii</i>	Pteropidae	13	13	1	3	4	1	0	1	4	4	0
Tolerant	topknot pigeon	<i>Lopholaimus antarcticus</i>	Columbidae	6	28	31	42	73	3	1	4	46	28	1
	common koel	<i>Eudynamys scolopacea</i>	Cuculidae	17	22	19	6	25	5	3	8	18	14	0
	channel-billed cuckoo	<i>Scythrops novaehollandiae</i>	Cuculidae	7	8	6	0	6	0	0	0	2	2	0
	little wattlebird *	<i>Anthochaera chrysoptera</i>	Meliphagidae	6	6	3	0	3	3	0	3	3	3	0
	Lewin's honeyeater	<i>Meliphaga lewinii</i>	Meliphagidae	48	398	82	24	106	19	3	22	78	43	20
	ped currawong	<i>Strepera graculina</i>	Artamidae	38	161	32	18	50	9	1	10	30	20	1
	satin bowerbird	<i>Ptilonorhynchus violaceus</i>	Ptilonorhynchidae	7	10	58	48	106	9	3	12	79	48	12
flying-foxes ³	<i>Pteropus</i> spp.	Pteropidae	39	201	26	22	48	6	2	8	30	23	0	
Increaser	black-faced cuckoo-shrike	<i>Coracina novaehollandiae</i>	Campephagidae	10	33	10	0	10	5	0	5	6	5	1
	figbird	<i>Sphecotheres viridis</i>	Oriolidae	41	465	49	25	74	13	4	17	48	27	8
	Australian magpie	<i>Gymnorhina tibicen</i>	Artamidae	26	121	1	0	1	4	1	5	1	1	0
	Torresian crow	<i>Corvus orru</i>	Corvidae	35	144	9	1	10	5	1	6	6	5	0
	silveryeye *	<i>Zosterops lateralis</i>	Zosteropidae	20	144	35	1	37	15	2	17	27	19	3
				Mean	28.6	17.9	46.5	6.7	1.1	7.8	31.8	19.6	-	
				SE	5.5	4.3	9.0	1.2	0.3	1.4	6.4	3.5	-	
				Total	134	87	221	25	11	36	146	62	-	

¹ From Moran et al. (2004a) (birds) or Moran (2007) (bats); comparisons of abundance in extensive forest (E), remnants (M) and regrowth (G); Decreasers' abundance pattern is E>M>G except for *A. crassirostris* (E=M>G); Tolerant pattern is E=M=G; Increasers' pattern is E=M<G except for *G. tibicen* (E<M<G).

² Bird species' nomenclature follows Christidis and Boles (1994). * species have small (<10 mm) gapes.

³ data for grey-headed (*Pteropus poliocephalus*) and black flying-foxes (*P. alecto*) were combined.

⁴ The total number of sites in which each frugivore species was present during surveys (max. possible = 48) and total number of individuals (Indivs) recorded during all surveys (four bird surveys, one bat survey in each site).

Table 2

Plant family	No. in data set	Average number consumed			Spearman rank correlation	
		Decreasers	Tolerant	Increasesers	R_s	P
Areaceae	5	1.8	1.3	0.6	0.40	0.05
Elaeocarpaceae	6	3.3	2.5	1.4	0.35	0.08
Euphorbiaceae	8	0.8	2.0	1.8	-0.20	0.22
Lamiaceae	5	1.3	0.6	0.0	0.50	0.02
Lauraceae	21	12.8	4.9	2.0	0.61	0.005
Meliaceae	7	2.8	2.0	0.6	0.44	0.04
Moraceae	13	8.0	7.8	5.8	0.23	0.19
Myrtaceae	19	6.5	5.1	1.0	0.53	0.02
Oleaceae	5	1.5	0.8	0.4	0.36	0.08
Rubiaceae	10	3.0	0.6	0.2	0.64	0.003
Rutaceae	10	2.8	1.4	0.8	0.43	0.04
Sapindaceae	15	2.5	3.0	3.0	-0.07	0.39
Vitaceae	6	4.3	2.3	0.2	0.69	0.001

Table 3

	Decreaser frugivores			
	<i>P. magnificus</i>	<i>P. superbis</i>	<i>P. regina</i>	<i>A. crassirostris</i>
Decreaser frugivores				
<i>Ptilinopus magnificus</i>	·	80	70	55
<i>P. superbis</i>	25	·	23	15
<i>P. regina</i>	64	68	·	51
<i>Ailurioedus crassirostris</i>	70	64	72	·
Tolerant frugivores				
<i>Lopholaimus antarcticus</i>	73	68	68	56
<i>Eudynamys scolopacea</i>	19	16	22	16
<i>Scythrops novaehollandiae</i>	7	8	7	5
<i>Anthochaera chrysoptera</i>	0	0	0	1
<i>Meliphaga lewinii</i>	38	40	49	46
<i>Strepera graculina</i>	41	48	42	35
<i>Ptilonorhynchus violaceus</i>	58	52	61	66
<i>Pteropus</i> spp.	36	27	31	34
Increaser frugivores				
<i>Coracina novaehollandiae</i>	6	8	7	8
<i>Sphecothes viridis</i>	44	52	53	40
<i>Corvus orru</i>	9	8	9	9
<i>Zosterops lateralis</i>	12	24	18	18
<i>Gymnorhina tibicen</i>	1	0	1	1
Fruigvore groups				
<i>L. antarcticus</i> & <i>P. violaceus</i>	80	72	78	81
Tolerant spp. (excluding <i>L. antarcticus</i> & <i>P. violaceus</i>)	59	64	66	58
Tolerant & Increaser spp. (excluding <i>L. antarcticus</i> & <i>P. violaceus</i>)	64	68	70	63
all Tolerant spp.	86	80	86	86
all Increaser spp.	46	56	55	48
all Tolerant & Increaser spp.	86	80	86	88

e.g., the top right cell of the table show that *P. magnificus* is known to eat 55% of the plants recorded in the diet of *A. crassirostris*. For non-decreaser species, only the percentage of plant species in each decreaser's diet that they share is shown.

List of figures

Figure 1 Classification of frugivore species (based on Bray-Curtis similarity matrix and UPGMA sorting) according to presence / absence of native plant species in the diet. Symbols next to names show the fragmentation response pattern for each frugivorous bird species. *Anthochaera chrysoptera*, *Gymnorhina tibicen* and *Nyctimene robinsonii* were not included because less than five native plant species had been recorded in their diets.

Figure 2 The proportion of native plant species with large (≥ 10 mm) diaspores that were consumed by decreaser, tolerant and increaser species. Only species with gape widths > 10 mm are included (see Table 1). Among tolerant species, data points for *Lopholaimus antarcticus* (*Lopant*), *Ptilonorhynchus violaceus* (*Ptivio*) and *Pteropus* spp (*Ptespp*) are highlighted.

Figure 3 The number of native plant species consumed by decreaser, tolerant and increaser frugivore species, for plant families where there was a significant ($p < 0.05$) association between frugivore species' sensitivity to fragmentation and the number of plant species consumed (see Table 2). Among tolerant species, data points for tolerant *Lopholaimus antarcticus* (*Lopant*), *Meliphaga lewinii* (*Mellew*), *Strepera graculina* (*Strgra*), *Ptilonorhynchus violaceus* (*Ptivio*) and *Pteropus* spp (*Ptespp*) and increaser *Sphocotheres viridis* (*Sphvir*) are highlighted where these are within the range shown by decreaser species.





