

1 **Conservation value of secondary forest habitats for endemic birds, a perspective**
2 **from two widely separated tropical ecosystems.**

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25 **Abstract:** Tropical secondary forests are increasingly widespread, but their potential
26 for conserving endemic birds remains unclear. Previous studies report different
27 results; however all have been restricted to geographically discreet locations. This is
28 important as different ecosystems are influenced by different external factors,
29 possibly influencing conservation potential. Here we use consistent survey methods to
30 examine how endemic bird richness varies between primary and secondary forest
31 habitats in two widely separated tropical ecosystems, providing a more global context
32 for evaluating the conservation value of secondary forests. Research was completed in
33 Lambusango Forest Reserve (LFR) on Buton Island, Sulawesi, and Cusuco National
34 Park (CNP), a Honduran cloud forest reserve. Bird communities in both forests were
35 surveyed using 50m radius point counts. Vulnerability assessments based on
36 ecological theory on avifaunal assemblages were then conducted, which suggested
37 endemics in LFR to be more susceptible to disturbance than those in CNP. Contrary
38 to the results from our vulnerability assessments, endemics in CNP were less tolerant
39 of moderate habitat modification than those in LFR. Richness of Mesoamerican
40 endemics per study site declined significantly between core zone forest (6.34 ± 0.81)
41 and more degraded forest in the boundary zone (3.86 ± 0.69). Richness of Wallacean
42 endemics was similar in primary (4.89 ± 1.68) and disturbed secondary forest ($4.52 \pm$
43 1.62). We recommend considering local and regional biogeographical and ecological
44 factors when determining the conservation value of secondary forests, and suggest
45 examples of potential importance, including differential community richness,
46 influence of figs and human settlement patterns.

47

48 **Key words: Avifauna; Biogeography; Endemism; Extinction; Mesoamerica;**

49 **Wallacea**

50 **INTRODUCTION**

51

52 Secondary forest ecosystems are expanding rapidly across the tropics, re-colonising
53 and replacing primary forests that have been destroyed or degraded by human activity
54 (Wright 2010; Dent and Wright 2009; Perz and Skole 2003). These secondary forests,
55 along with other regenerating or degraded habitats, are expected to become an
56 increasingly prominent feature of tropical landscapes in the 21st century, and their
57 expansion will have strong implications for the conservation of biodiversity (Dent and
58 Wright 2009). Consequently, numerous studies to examine the capacity of these
59 forests for retaining a high diversity of organisms have been completed. Many of
60 these studies have focussed on birds, as they are relatively easy to sample and because
61 their good ecological congruence with other taxonomical groups allows them to be
62 used, to a certain extent, as ecological indicators for biodiversity as a whole (Gardner
63 et al. 2008; Howard et al. 1998). The results of these studies have varied considerably;
64 some suggest that secondary forests, particularly older stands or those adjacent to
65 more pristine ecosystems, have a high conservation potential for birds, supporting
66 similar avian richness to that of primary forest (O’Dea and Whittaker 2007; Sodhi et
67 al. 2005) while others indicate these habitats to be no substitute for old-growth forest
68 for conserving most resident bird species (Gibson et al. 2011; Maglianesi 2010; Peh et
69 al. 2006).

70 While these studies have contributed significantly to understanding the conservation
71 value of secondary forest, at least two significant gaps in this understanding remain.
72 The first stems from the tendency of these previous research projects to draw
73 conclusions from results obtained from single study sites, each widely separated
74 geographically from the others. This could partially account for the conflicting results

75 reported; these different sites are likely to possess bird communities with different
76 species assemblages and be influenced by different ecological and biogeographical
77 factors, perhaps facilitating a higher tolerance of disturbance in some communities
78 than in others (Gibson et al. 2011). The second gap stems from most previous studies
79 focussing largely on avian richness as a whole; this is important as some avian
80 subgroups are considered less tolerant of habitat modification than others. Endemic
81 birds with restricted ranges are considered particularly at risk, many being adapted to
82 highly specialised, local habitats created by the same biogeographical factors
83 facilitating evolutionary isolation and endemism (Jankowski and Rabenold 2007;
84 Trevino et al. 2007), thus possessing narrow ecological tolerances. Additionally,
85 because their small populations and limited ranges facilitate an inherently greater
86 extinction risk they often represent a higher conservation priority compared with
87 wider ranging species (Pimm and Raven 1997). The capacity of secondary forests to
88 support endemic birds, and the variation of this capacity on a global scale and across
89 ecosystem types, therefore require further research.

90 In this study we aim to examine the value of tropical secondary forests for endemic
91 bird species from a global perspective, testing the hypothesis that these habitats can
92 possess higher conservation potential in some areas than others depending on the
93 composition of ecological communities and the influence of local biogeographical
94 factors. To do this we examine how richness of endemic bird species varies between
95 primary forest and a variety of secondary forest habitats in two endemic-rich, but very
96 different and geographically separated, forest ecosystems with very different bird
97 communities; an area of lowland seasonal forest located on a small island within the
98 Wallacean region of Indonesia, and an area of neotropical cloud forest in North-West
99 Honduras. Species richness analysis rather than abundance estimates form the focus in

100 this study as these are more concise and less prone to detection error and bias (Riddle
101 et al. 2010; Karr et al. 1990), although information on abundance variations in our
102 two study sites can be found elsewhere (Martin and Blackburn 2010b; Martin and
103 Blackburn 2009). We first examine the composition of endemic bird assemblages in
104 these two different ecosystems and assess which assemblage will be theoretically least
105 tolerant of secondary forest ecosystems, based on ratios of 'high risk' species with
106 low ecological tolerances. We then examine how endemic richness actually varies in
107 differentially disturbed forest types in each location. We then attempt to interpret our
108 results with consideration to local ecological and biogeographical influences.

109

110 **METHODS**

111

112 **Study sites**

113 Our two widely-separated forest ecosystems were located in the biodiversity
114 'hotspots' of Wallacea and Mesoamerica (Myers et al. 2000), both noted for
115 possessing high proportions of endemic species with high conservation importance, as
116 well as facing high rates of habitat modification (Conservation International 2011;
117 Stattersfield et al. 1998).

118 The Lambusango Forest Reserve (5°10'S, 122°24' E), subsequently referred to as
119 LFR, is a 65,000 ha area of lowland tropical forest located on Buton Island, off the
120 South-East coast of Sulawesi in the Indonesian archipelago (Fig. 1a). The reserve is
121 divided into a 28,510 hectare strict forest reserve and a 35,000 hectare production
122 forest (Singer and Purwanto 2006). A total of 79 bird species have been recorded
123 here, 37 (47%) being regional endemics (Martin et al. 2012).

124 Cusuco National Park (15°29.8'N, 88°13W), subsequently referred to as CNP, is a
125 23,440 ha protected area of tropical montane cloud forest located in North-Western
126 Honduras (Fig. 1b). It is divided into a 7,690 ha core zone where most human
127 activities are nominally restricted, and an encompassing 15,750 ha buffer zone where
128 some controlled land-use is permitted (Lenkh 2005). Elevation ranges from 500 –
129 2200m above sea-level. CNP has a rich avifauna with 209 recorded species, 44 (21%)
130 being Mesoamerican endemics (Martin et al. 2009).

131

132 **Theoretical vulnerability assessment**

133 An assessment to predict which of the two bird communities would be least tolerant
134 of secondary forest ecosystems was completed based on ecological theory and
135 community composition in our two study sites. We collated species lists of the known
136 avifauna of LFR and CNP (Martin et al. 2012; Martin and Blackburn 2010a), and
137 compared ratios of species with different body sizes and within certain feeding guilds.
138 Body size was examined as large-bodied birds are considered particularly susceptible
139 to local extirpation from habitat disturbance due to their requiring large habitat
140 patches, tending to occupy higher trophic levels and possessing lower reproductive
141 rates than smaller-bodied species, all of which have been shown to increase
142 vulnerability to local extinction (Sodhi et al. 2004; Gaston and Blackburn 1995).
143 Certain avian feeding guilds have also been hypothesized to be more susceptible to
144 habitat modification than others. Diversity of forest frugivores is strongly linked to
145 the richness of fruiting plant species, which are most diverse in undisturbed forest
146 ecosystems, and birds of this feeding guild often require large foraging areas due to
147 the spatial and temporal scarcity of year-round fruit resources; thus degradation of
148 forest ecosystems impacts strongly upon these species (Gray et al. 2009; Sodhi et al.

149 2004). Insectivores have likewise been considered to be strongly affected by habitat
150 modification and fragmentation due to their dependence on specific foraging
151 microhabitats and possessing limited dispersal capabilities (Sodhi et al. 2004).

152 Differences in body size were examined by comparing average body length (cm) of
153 all endemic species with an unpaired t-test (Zar 1999). We also compared proportions
154 of large birds with a body length of > 30cm using a χ^2 test (Zar 1999). Measurements
155 of mass rather than length would have been preferable, but data describing the body
156 mass of most Wallacean species do not occur in the literature. Differences in feeding
157 guild compositions were examined by calculating the ratio of frugivores and
158 insectivores compared to endemic bird assemblages as a whole.

159 These analyses were applied to comparisons of both Wallacean/Mesoamerican
160 hotspot endemics, and also between Wallacean endemics and 'highland endemics'.
161 This separate analysis only included endemic species defined by Howell and Webb
162 (2005) as occurring at an altitudinal range of >1000m, and only sites occurring within
163 this altitudinal zone were included, thus reducing altitudinal influence on our results.

164

165 **Sampling sites**

166 A total of 84 single point count study sites were surveyed in LFR, spread equally over
167 three areas of differentially disturbed forest. These areas corresponded approximately
168 to areas of near-pristine primary forest, well-regenerated secondary forest subjected to
169 agricultural clearance and logging until the establishment of the LFR conservation
170 area in 1975, and heavily-disturbed secondary forest in the reserve's periphery which
171 has been recently subjected to intermittent logging and shifting cultivation. Both areas
172 of secondary forest were in close proximity to, and spatially contiguous with, tracts of
173 undisturbed primary forest. These forest categories were first identified by visual

174 observations and research into local ecological history, and then characterised
175 empirically by completing vegetation surveys at each site (see below). Study sites
176 were located at 150m intervals along 900m linear transects, each spaced 1km apart.
177 Four transects were located in each forest type, with seven study sites located along
178 each transect. Further details of these study sites, along with a map displaying their
179 location within the reserve, can be found in Martin and Blackburn (2010b).

180 A total of 126 single point count study sites were surveyed in CNP. These were
181 scattered across the park's different management zones along non-linear transects at
182 intervals of >200m. A total of 59 sites were located in the centre of the park's core
183 zone, at altitudes between 1450 – 2200m (subsequently referred to as 'deep core')
184 where no land use is nominally permitted, 39 points within transitional core zone
185 areas close to the buffer/core boundary between 1350 – 1700m ('boundary core') and
186 28 points in the buffer zone at altitudes of 700 – 1450m ('buffer zone'). This buffer
187 experiences the greatest environmental pressure, as several thousand people live
188 within or just outside its borders and land-use regulations are minimal (Lenkh 2005).
189 Further details describing the locations of these points can be found in Martin and
190 Blackburn (2009).

191

192 **Bird sampling**

193 Endemic bird assemblages at both locations were surveyed using 50m circular plot
194 point counts, this relatively small radius reduced the influence of differential
195 detectability between highly vocal and more cryptic species (Bibby et al. 2002).
196 Previous fieldwork experience in our study areas has also demonstrated that a 50m
197 radius yields little variation in detectability rates between primary and secondary
198 forest types in these locations. Sampling was conducted each morning between 06:00

199 - 08:00 in LFR and 06:00 - 09:30 in CNP, these being the periods where bird
200 detectability is highest in these regions (Marsden 1999; Wunderle 1994). Each count
201 lasted for 10 minutes, with all species seen and heard during each time being
202 recorded, excluding those flying above the canopy. Point counts were not carried out
203 in rain or heavy mist. Each point was surveyed twice in LFR and three times in CNP.
204

205 **Vegetation surveys**

206 Vegetation surveys were completed at each study point to provide inferential evidence
207 of forest disturbance levels across each of our locations. All variables were measured
208 within a 20m radius of the points centre in LFR, and within a 20mx20m grid
209 surrounding the central point in CNP. Canopy cover was evaluated at each point using
210 a canopy scope constructed from a perspex square marked with a 5X5 grid of dots
211 separated by 3cm (Brown et al. 2000). Five measurements were taken at each point
212 and the mean value calculated and converted into a proxy percentage value for each
213 forest type. The number of large trees with a diameter at breast height (dbh) of >50cm
214 was counted at each plot, and the mean number per plot in each forest type calculated,
215 along with the mean dbh of these trees. Undergrowth density was assessed differently
216 in each location. In LFR densities were estimated utilising a 1.5m measuring pole
217 marked with 50 black bands. A consistent observer counted the number of bands
218 visible at 10m at four points within each site, which was then doubled to a proxy
219 percentage value density estimate. Mean values for each forest type were then
220 calculated. In CNP density was assessed by placing a 0.5m pole vertically and
221 counting the number of times any vegetation made contact with it. This was repeated
222 32 times at each plot, with mean values calculated for each plot and for each forest
223 category as a whole, which were then converted into proxy percentage values.

224

225 **Statistical analysis**

226 The mean number of Wallacean endemic species in LFR, and both Mesoamerican
227 endemics and highland forest endemics in CNP, detected at sample sites across each
228 forest type were calculated and compared using Kruskal-Wallis one-way ANOVA
229 analysis (Zar 1999). Sample-based rarefaction curves plotting numbers of individuals
230 recorded against number of endemic species detected were calculated using the
231 software package EstimateS (Colwell 1997). A further series of nonparametric species
232 richness estimators were calculated utilising EstimateS; the mean value of these being
233 utilised as true species richness estimates, as the effectiveness of different estimators
234 is expected to vary with different data sets (Sodhi et al. 2005).

235

236 **RESULTS**

237

238 Results indicate that the endemic avifauna of LFR possess higher proportions of each
239 of the evaluated 'high-risk' categories compared to the avifauna of CNP. Mean body
240 length of endemic species in LFR (32.91cm) is significantly higher than that of both
241 Mesoamerican endemics (unpaired T-test $F = 6.315$, $p < 0.05$) and highland forest
242 endemics ($F = 4.817$, $p < 0.05$) in CNP (Table 1). Proportions of endemic birds with
243 a body length of >30 cm were also significantly higher in LFR than Mesoamerican (χ^2
244 $= 5.126$, $p < 0.05$) and highland forest ($\chi^2 = 7.021$, $p < 0.05$) endemics in CNP.
245 Endemic avifaunal assemblages in LFR also possess a greater proportion of both
246 frugivores (48% of species assemblage compared to 38.9/44.4%) and insectivores
247 (36.4% compared to 19.4/14.8%) than endemic and highland forest restricted avifauna
248 assemblages in CNP.

249 Vegetation survey results in Table 2 indicate that point-count survey sites
250 encompassed a similar variety of forest types in both LFR and CNP. The primary
251 forest sites surveyed in LFR correspond well with the deep and boundary core sites
252 surveyed in CNP as ‘high quality’ habitats, with the highest frequency and mean size
253 of large trees and sparsest understorey. Disturbed secondary forest in LFR
254 corresponds approximately with forest structure in CNP’s buffer zone, with a marked
255 reduction in the frequency and size of large trees and denser understorey, both being
256 representative of substantially modified secondary forest habitat. We therefore
257 considered it reasonable to use these habitat categories for comparing effects of
258 disturbance on endemic bird communities.

259 Point count surveys in LFR indicated that most endemic species were relatively
260 resilient to moderate habitat modification; the number of endemic species detected per
261 sample site was statistically similar in primary forest (4.89 ± 0.98) and disturbed
262 secondary forest (4.52 ± 0.98) (Kruskal-Wallis $H = 2.112$, $p = 0.348$) (Fig. 2a). This
263 was not true of all species; our previous study (Martin and Blackburn 2010b) showed
264 that populations of several large-bodied frugivores and insectivores were concentrated
265 in primary and regenerating secondary forest sites, with low densities occurring in
266 disturbed secondary forest. However, richness per site of endemic species as a whole
267 remains similar across all forest categories. Endemic avifauna communities in CNP,
268 however, appear to be more vulnerable to habitat modification, with the number of
269 endemic birds detected per sample dropping significantly (Kruskal-Wallis $H = 14.04$,
270 $p < 0.05$) between the boundary of core zone forest (6.34 endemic species per sample
271 site ± 0.81) and the buffer zone (3.86 endemic species per sample site ± 0.69) (Fig.
272 2b).

273 Results therefore suggest that some difference exists between endemic birds'
274 response to habitat disturbance in LFR and CNP. Non-parametric estimators in Table
275 3 and species rarefaction curves reproduced in Fig. 3 suggest this difference to be
276 even greater when comparisons are made between highland endemics in CNP and all
277 endemics in LFR. Species estimators for the LFR study sites demonstrate similar
278 results to those shown in Fig. 3, with species estimates in disturbed secondary forest
279 (21.59) being only slightly less than those in primary forest (24.91). Estimators for
280 CNP, however, demonstrate a marked drop in predicted richness estimates between
281 boundary core sites (26.22) and the sites at upper elevation in the buffer zone (11.69)
282 – a decline of >50%. Species accumulation curves in Fig. 3 display similar patterns,
283 with forest categories in LFR producing very similar trajectories while the buffer zone
284 curve in CNP levels out at a much lower number of species than the deep or boundary
285 core.

286

287 **DISCUSSION**

288

289 Comparisons of body size and feeding guild composition demonstrate that the
290 endemic avifauna of LFR has greater proportions of all evaluated 'high risk'
291 categories compared to endemic avifauna in CNP, therefore predicting the endemic
292 species of LFR to be less tolerant of modified secondary forest ecosystems than those
293 of CNP. This is further supported by extinction-risk theory. Wallacean endemics are
294 more evolutionarily distinct than those of Mesoamerica; Sulawesi alone possesses 14
295 unique genera of birds, compared to just two in montane regions of Northern Central
296 America, (neither of which occurs in CNP) (Stattersfield et al. 1998). It could
297 therefore be hypothesized that Wallacean island avifaunal communities might possess

298 a higher ratio of endemic species with greater specialization due to longer
299 evolutionary isolation, and therefore prove less tolerant to habitat modification than
300 Mesoamerica endemic bird communities. The theorized vulnerability of island
301 ecosystems with high endemism is indicated quantitatively by estimates that endemic
302 birds on oceanic islands are up to 40 times as likely to be threatened with extinction as
303 continental species (Trevino et al. 2007). Indeed, of the 101 bird species listed as
304 having become extinct since 1600 CE, 88 species (>87%) were island endemics, with
305 habitat modification being an important causality in many of these extinctions
306 (Johnson and Stattersfield 1990). Blackburn et al. (2004) also describe how the
307 greatest concentrations of these island extinctions occurred in archipelagos where bird
308 communities have experienced extensive periods of evolutionary isolation and
309 possess high rates of endemism to a genus level, a characteristic shared by Wallacean
310 avifauna.

311 It could be counter-argued that Mesoamerican cloud forests themselves represent
312 ‘continental islands’, being comprised of small, fragmented ecosystems surrounded
313 by a matrix of very different lowland habitats (Martinez-Morales 2005). However, a
314 matrix of non-forest may not present so formidable a barrier to many bird species as
315 ocean, especially as most Mesoamerican endemics appear to utilize a fairly wide
316 range of habitats. Of the 43 regional endemic species recorded in CNP, only seven
317 (16%) are found exclusively in cloud forest ecosystems (Howell and Webb 2005). A
318 further eleven species (26%) occur in a wide range of highland forest habitats >800m,
319 while the remaining 25 species (58%) occur in a wide range of forest habitats or are
320 generally associated with non-cloud forest lowland ecosystems; therefore the theory
321 of cloud forest as an ‘island’ habitat is not directly applicable for most endemic
322 species in CNP.

323 However, results from our surveys across differentially disturbed forest types show
324 that despite possessing theoretically greater vulnerability to habitat modification,
325 endemic birds in LFR were in actuality significantly less impacted by moderate
326 disturbance than Mesoamerican and highland forest endemics in CNP. The response
327 of endemic birds to habitat disturbance in CNP appears to concur with deterministic
328 theories concerning the vulnerability of range-restricted species (Trevino et al. 2007;
329 Pimm and Raven 1999). Species richness of endemic and cloud-forest restricted
330 species declines markedly between high quality core zone forest and more degraded
331 secondary forest habitats in the buffer zone. The sensitivity of endemics to habitat
332 modification has been reported widely across the neotropics (Barlow et al. 2007;
333 Gardner et al. 2007), tropical Africa (Burgess et al. 2002; Fjeldsa 1999) and
334 continental South-East Asia (Peh et al. 2008, 2005).

335 Endemic bird communities in LFR, however, do not display the same response.
336 Similar richness of endemic birds was reported in degraded secondary forest and
337 primary forest, with persistence of endemics only seeming to drop markedly in
338 heavily modified cleared farmland sites (Martin and Blackburn 2010b). The
339 accommodation of endemic species in disturbed ecosystems on mainland Sulawesi
340 has also been reported elsewhere (Sodhi et al. 2005; Thiollay and Rahman 2002).

341 It therefore appears that our initial theoretical assessment of the relative
342 vulnerabilities of endemic birds in these two forest ecosystems does not match the
343 actual results derived from fieldwork surveys, and that, in actuality, endemic bird
344 species in LFR appear to be more tolerant of secondary forest ecosystems than those
345 of CNP. The reasons for this difference pose an important research question, given the
346 theorised higher vulnerability of endemic avifauna in LFR. A number of potential

347 ecological and biogeographical factors could contribute to these apparent differences
348 in ecological vulnerabilities, which we consider below.

349

350 **1 - Differential species richness**

351

352 One possible control contributing towards differential endemic avifaunal response to
353 disturbance could result from substantial differences in total avian richness between
354 the study sites. A total of 79 species are known to occur in LFR, including 37 regional
355 endemics (Martin et al. 2012), compared to 209 species in CNP, with 21% being
356 Mesoamerican endemics and 12% highland forest endemics (Howell and Webb
357 2005). CNP therefore has a lower overall ratio of endemic: non-endemic species, and
358 over four times as many bird species in a spatial area less than half the size of LFR
359 (23,440 hectares vs 65,000 hectares). The relatively depauperate species richness of
360 bird communities in LFR is characteristic across all Wallacean islands (Coates and
361 Bishop 1997), especially when compared to avian richness on islands immediately to
362 the east and west of the region (Table 4). Relatively low species diversity may result
363 in lower niche competition, therefore endemics here may need to be less specialised
364 and thus could be more tolerant of habitat modification. Low niche competition may
365 be further influenced by low richness within most avian families within LFR. Table 4
366 shows how 65% of bird families with at least one endemic species in LFR have ≤ 3
367 species represented, and only three families are represented by >4 species. Low
368 species richness in families represented by endemics is also characteristic of the
369 avifauna of Sulawesi generally; Table 4 shows that families represented by endemic
370 species in LFR have consistently far fewer species represented across the island
371 compared with comparable biogeographical regions bordering Wallacea. With one

372 exception (Coraciidae), the Australasian families generally have far higher species
373 diversity in New Guinea, and Oriental families typically have a higher species
374 diversity across the Makassar Straits in Borneo. As niche competition is often greatest
375 within species of the same family sharing similar habitat and dietary requirements
376 (Graves and Gottelli 1993), the low number of species in each family may result in
377 low inter-species competition, allowing endemics to be less specialised. The potential
378 for a lack of specialisation among LFR endemics may also be inter-related to Butons'
379 status as a relatively small, species depauperate island (White and Bruce 1986). It
380 could be that many of the endemics found in LFR had to be fairly unspecialised in
381 order to be able to successfully colonise the island in the first place, in the manner of
382 supertramp species (Diamond 1974). The endemic species assemblage in LFR
383 contains few species usually considered as supertramps, although there is a high
384 representation of species in groups known to be effective island colonisers (e.g. large-
385 bodied pigeons and White-eyes). Certain endemics have also been considered very
386 closely related to, or conspecific with, known supertramps, such as the relationship
387 between *Ducula luctuosa* and *Ducula bicolor* (Sibley and Monroe 1990). Thus
388 colonisation history should also be considered as a factor with regards to a potential
389 lack of specialisation among LFR endemics.

390

391 **2 - High vegetation diversity in the Lambusango**

392

393 While the richness of most faunal groups in Wallacea is low, diversity of plants,
394 which have not been inhibited from colonizing by the region's biogeographical
395 barriers (Whitten 2002), is remarkably high, and this may also facilitate resilience of
396 endemic avifauna to moderate anthropogenic disturbance in LFR. While most South-

397 East Asian forest ecosystems are characteristically dominated by a single family of
398 trees, Dipterocarps (Corlett and Primack 2005), forests on Sulawesi are highly
399 diverse, with no plant families being predominant (Whitten et al. 2002). No
400 comprehensive survey of plant diversity on Sulawesi has yet been conducted,
401 although Kessler et al. (2005) described how a single hectare plot of sub-montane
402 primary rainforest in Central Sulawesi possessed 148 tree species comprised of 82
403 genera and 42 families. This represents a diversity considerably greater, particularly at
404 a family level, than research at comparable sample sites have demonstrated to exist in
405 other areas of insular South-East Asia (Hamann et al. 1999). This high floristic
406 diversity may have created ecosystems with a wide variety of trophic niches and
407 microhabitats, to which endemic avifauna may by necessity have adapted. As they
408 could already be adapted to a diverse floristic structure, they might be more resilient
409 to changing habitats caused by anthropogenic modification. Species-rich plant
410 assemblages are not unique to Wallacea; Mesoamerican cloud forests also possess
411 rich and diverse floral assemblages (Nadkarni et al. 1995). However, the hypothesis
412 that high floral diversity may contribute to the apparent tolerance of Wallacean
413 endemic bird to secondary forest ecosystems may warrant further consideration.

414

415 **3 - Presence of strangler figs as a food resource in degraded forest habitats**

416

417 Another factor to consider with regard to differences in adaptability to secondary
418 forests demonstrated by endemics between the two communities concerns the
419 difference in the trophic composition of bird communities between the two hotspots
420 and the persistence of strangler figs in degraded forest habitats in Sulawesi. Figs are
421 highly important food resources for frugivorous birds in both South-East Asia and the

422 neotropics, and strangler figs, a subgroup of the *Ficus* genus, have been noted as
423 particularly important, producing substantially larger crops than non-strangler fig
424 species (Walker 2007). These can provide >50% of the total diet of frugivorous
425 species in the tropics (Corlett and Primack 2005). Figs are therefore considered a
426 ‘keystone’ resource for tropical frugivores, but are perhaps particularly important in
427 Wallacea, firstly because Wallacean figs are especially productive, producing up to
428 five times as much fruit mass as species in other parts of South-East Asia (Kinnaird
429 and O’Brien 2005), and secondly because frugivores constitute a high percentage of
430 endemic bird assemblages here – nearly 50% of Wallacean endemics are primarily
431 frugivorous (Coates and Bishop 1997).

432 Strangler figs occur at low densities throughout LFR, including in degraded secondary
433 forest which otherwise has few large, fruiting tree species, possibly because the wood
434 of these figs is less valuable as a timber resource than other hardwoods, and as such
435 may have been left intact by loggers. Stranglers could therefore be an important resource
436 for frugivores in disturbed landscapes where other food sources are scarce. As
437 frugivores constitute such a large proportion of endemic bird species in LFR, this
438 could contribute to the nearly equal numbers of endemic species in primary and
439 disturbed secondary forest here. Other non-frugivorous endemic species may also
440 benefit from strangler figs, providing roosting and nesting sites in landscapes where
441 other large trees are scarce.

442 The importance of strangler figs as a resource for endemic frugivores in degraded
443 forests may also be implicated by our results from CNP. Strangler figs here are
444 largely confined to areas of less disturbed forest in the core zone, and are scarce in the
445 buffer zone where richness of endemic species, many of which are frugivores (38.9%)
446 (Howell and Webb 2005), is also low. We acknowledge, though, that other important

447 resources for neotropical frugivores exist, especially fruiting trees in the Lauraceae
448 family (Wheelwright 1986), and as these remain unmapped in CNP their role for
449 supporting species in secondary forest remains unknown.

450

451 **4 – History of human settlement**

452

453 A final factor which may contribute to differential responses in the two study sites
454 relates to historical patterns of human settlement. Globally, the distribution of
455 endemic birds is largely concentrated in the two broad ecosystem types examined in
456 this paper, oceanic islands and montane forest. A review of Stattersfield et al.'s (1998)
457 218 endemic bird areas show that 74% consist solely of these habitat types, which
458 together encompass the entire ranges of >80% of all range-restricted bird species.
459 These endemic-rich ecosystems also coincide with areas of comparatively late human
460 colonization, as biogeographical factors promoting speciation and endemism have
461 also acted as barriers human immigration. While humans had successfully colonised
462 most major landmasses and started to modify their environments by the beginning of
463 the Neolithic revolution (Roberts 1998), this impact was not felt in many centres of
464 avian endemism until comparatively recently, with most endemic-rich island groups
465 avoiding colonisation until the mid-Holocene or later (Roberts 1998) (Table 5).

466 Most montane forests were also spared heavy anthropogenic modification until
467 relatively recently. While records of ancient agriculture in lower-montane slopes do
468 exist in some regions (Denham et al. 2003), most areas of mountainous forest,
469 particularly at mid-high elevations, were much less impacted by early agriculture than
470 lowland areas due to unfavourable topography, accessibility and climate (Roberts
471 1998). This appears to be the case in Mesoamerica; while complex agrarian societies

472 have existed here since at least 5000 BP, most have been centred in lowland areas
473 (Bray and Klepis 2005). Much of the region's cloud forest, including that found in
474 CNP, was left relatively undisturbed until as recently as the mid-20th century, when
475 modern infrastructure made these regions accessible (Bray and Klepis 2005).

476 Most centres of avifaunal endemism therefore correspond with ecosystems which
477 have been isolated from anthropogenic disturbance until comparatively recently,
478 leading to resident endemic birds inhabiting habitats with relative long-term stability
479 and, in the case of oceanic islands, low competition environments with little predation
480 or hunting pressure. The recent appearance of humans and associated habitat
481 modification after long periods of ecological isolation may therefore have had a
482 disproportionately heavy impact on these species adapted to ecosystems which have
483 probably been little changed since the early Holocene (Bush et al. 2004).

484 The Wallacean region, however, along with neighbouring New Guinea, represents
485 one of the few areas where a high concentration of endemic bird species coincides
486 with a long history of human settlement. Evidence suggests modern humans have
487 been present on Sulawesi since at least 30,000 BP, (Whitten et al. 2002) (Table 5).
488 with swidden-system farming here dating back at least to 4000 BP, and as far back as
489 6,500 BP on New Guinea (Denham et al. 2003; Whitten et al. 2002). Continual
490 cultivation and associated disturbance of forest ecosystems for most of the Holocene
491 may be long-term enough for species to have adapted to this as an almost integral
492 ecological process. While modern forest disturbance is of an entirely different
493 magnitude to that caused by pre-industrial cultivation patterns, long-term low-level
494 habitat modification may have facilitated the adaptation of species to secondary forest
495 habitats. This could have a bearing on why numerous studies have shown Wallacean
496 endemics to be fairly tolerant of moderate habitat disturbance. This could perhaps be

497 linked to Brook and Bowman's (2002) broader hypothesis concerning survival of
498 megafauna in areas with long-term human presence, such as in Africa, where slow
499 adaptation to anthropogenic activity was possible.

500

501 **CONCLUSION**

502

503 This study suggests that the conservation value of secondary forests for supporting
504 endemic birds can vary in different tropical forest habitats in different parts of the
505 globe, and that ecological and biogeographical factors may be important influences in
506 determining the tolerance of endemic species to modified habitats. The mechanisms
507 invoked in this study to explain why endemic birds in LFR are less impacted by
508 moderate disturbance of forest ecosystems than those in CNP represent only a limited
509 range of potential factors that could influence the ecological tolerances of endemic
510 species; other variables such as climatic regimes and frequency of natural disturbance
511 events, for example, may be worthy of consideration as well. The key finding of this
512 study, however, is that tropical secondary forest ecosystems are unlikely to be
513 uniformly 'valuable' or 'invaluable' habitats for the conservation of endemic bird
514 species in the future. The capacity of secondary forests for supporting these species is
515 likely to be strongly influenced by a range of local or regional biological and
516 geographical variables, and these need to be taken into account when assessing the
517 conservation potential of these habitats in the future.

518

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520

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525

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747 *Table 1 - Comparison of characteristics of endemic bird assemblages in the Lambusango forest*
 748 *reserve, Buton Island, South-East Sulawesi, and endemic and highland-restricted species in Cusuco*
 749 *National Park, Honduras. N represents sample size. Categories compared are mean body length (cm)*
 750 *the percentage of endemic species with a body length of >30cm, and the proportion of frugivores,*
 751 *insectivores and other feeding guilds in each avifauna community. Bracketed numbers indicate total*
 752 *number of species represented in percentage values. Measurements and feeding guild information*
 753 *based on Coates and Bishop (1997) and Howell and Webb (2005).*
 754

		Mean body	% N body length			
	N	length (cm)	>30cm	% Frugivores	% Insectivores	% Other
Lambusango endemic						15.15
species	33	32.91	51.52 (17)	48.5 (16)	36.4 (12)	(5)
Cusuco endemic						41.7
species	36	21.06	16.7 (6)	38.9 (13)	19.4 (7)	(15)
Cusuco highland-						40.7
restricted species	27	20.63	14.8 (4)	44.4 (12)	14.8 (4)	(11)

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767 *Table 2 - Vegetation variables in a) primary forest, regenerating secondary forest and disturbed*
 768 *secondary forest in the Lambusango Forest Reserve, South East Sulawesi, and b) deep core, boundary*
 769 *core and buffer zone sites in Cusuco National Park, Honduras. ± indicates variance to 1 standard*
 770 *deviation.*

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772 **a)**

	Mean canopy cover (%)	Mean frequency of large trees (>50cm dbh diameter)	Mean dbh of large trees (cm)	Undergrowth density (%)
Primary forest	83.92 ± 5.08	4.8 ± 1.89	83.9 ± 35.2	17.17 ± 5.1
Regenerating secondary forest	81.36 ± 5.2	2.1 ± 0.9	68.77 ± 18.32	24.4 ± 0.7
Disturbed secondary forest	74.56 ± 6.92	2.3 ± 1.1	61.763 ± 15.2	17.8 ± 1.6

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774 **b)**

	Mean Canopy cover (%)	Mean frequency of large trees (>50cm dbh diameter)	Mean dbh of large trees (cm)	Undergrowth density (%)
Deep core	89.5 ± 5.85	14.4 ± 7.69	108.56 ± 22.62	1.4 ± 0.64
Boundary core	90.4 ± 6.34	17.61 ± 7.06	105 ± 28.7	1.72 ± 0.41
Buffer zone	88.59 ± 8.95	7.85 ± 4.4	83 ± 18.01	1.6 ± 0.59

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782 Table 3 - Non-parametric species estimators for a) primary forest, regenerating secondary forest,
 783 disturbed secondary forest and cleared agricultural land within the Lambusango forest reserve, Buton
 784 Island, South-East Sulawesi, and b) deep core, boundary core and buffer zone sites within Cusuco
 785 National Park, Honduras. *n* represents sample size. *Sp obs* and *Ind obs* represent total number of
 786 species and individuals observed, respectively. ACE, ICE, CHAO1, CHAO2, Jack1, Jack2, Bootstrap,
 787 MMRuns and MMMeans are non-parametric species estimators (Colwell and Coddington, 1994).

788 a)

Parameters	Primary	Regenerating secondary	Disturbed secondary
N	28	28	28
Sp obs	22	22	20
Ind obs	287	243	214
ACE	24.07	24.63	20.27
ICE	24.45	23.97	20.91
Chao1	25	22.75	21.62
Chao2	23.47	23.96	20.91
Jack1	25.92	25.92	21.96
Jack2	26.94	27.89	20.1
Bootstrap	24.01	23.78	21.44
MMRuns	25.1	24.55	23.49
MMMeans	25.23	24.47	23.63
Average species estimate	24.91	24.66	21.59

789

790 b)

Parameters	Buffer >1000	Boundary Core	Deep core
N	28	39	59
Sp obs	11	23	23
Ind obs	106	539	880
ACE	11	29.17	24.27
ICE	11	29.02	24.25
Chao1	11	24.66	23.16
Chao2	11	24.65	23.16
Jack1	11	27.95	24.98
Jack2	11	27.99	24.05
Bootstrap	11.47	25.51	24.55
MMRuns	14.08	23.09	23.07
MMMeans	13.73	23.99	23.12
Average species estimate	11.69	26.22	23.85

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795 *Table 4 - Comparison of richness of avifaunal families represented by at least one endemic species in*
796 *the Lambusango Forest Reserve, Buton Island, South-East Sulawesi with richness of these families to*
797 *the West of Wallacea in Borneo and to the East in New Guinea. Families listed as having centre of*
798 *diversity as Australasian have greatest number of species occurring East of Lydekkers' line. Families*
799 *listed as having centre of diversity as Asian have greatest number of species occurring West of*
800 *Wallace's line (Coates and Bishop 1997). Cosmopolitan families are evenly distributed across the*
801 *Oriental and Australasian zoogeographical zones. Species list for Sulawesi based on Coates and*
802 *Bishop (1997). Species list for Borneo and New Guinea based on Clements (2007).*

803

Family	Centre of diversity	Endemics in Lambusango	Species in Lambusango	Species in Sulawesi	Species in Borneo	Species in New Guinea
Accipitridae	Cosmopolitan	3	4	18	31	33
Columbidae	Australasia	3	8	24	20	56
Psittacidae	Australasia	5	6	10	5	51
Cuculidae	Cosmopolitan	2	5	15	22	20
Centropidae	Cosmopolitan	1	1	2	3	5
Tytonidae	Australasia	1	1	4	1	7
Strigidae	Cosmopolitan	1	1	3	12	9
Coraciidae	Asia	1	1	2	1	1
Bucerotidae	Asia	2	2	2	8	1
Picidae	Asia	1	1	2	18	0
Campephagidae	Australasia	3	3	10	11	18
Corvidae	Cosmopolitan	1	2	2	8	4
Timallidae	Asia	1	1	2	35	0
Petroicidae	Australasia	1	1	1	0	23
Sturnidae	Asia	3	4	11	7	11
Dicaeidae	Asia	2	2	3	12	6
Zosteropidae	Cosmopolitan	1	2	7	7	11

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811 *Table 5 – Approximate dates of human colonisation of oceanic archipelagos with high rates of*
812 *avifaunal endemism.*

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Island group	Date of colonisation (BP)	Source
Lesser Sundas	100,000	Whitten <i>et al.</i> 2002
New Guinea	>50,000	O' Connell & Allen 2003
Sulawesi	> 30,000	Whitten <i>et al.</i> 2002
Lesser Antilles	5,000	Keegan & Diamond 1987
Madagascar	2000	Burney <i>et al.</i> 1997
Hawaii	1400	Keegan & Diamond 1987
New Zealand	800	McGlone 1989
Mascarenes	400	Keegan & Diamond 1987

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831 **Figure Legends**

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834 Figure 1 – Maps showing the locations of **A)** Buton Island within the Indonesian
835 archipelago, and **B)** Cusuco National Park in Central America.

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837 Figure 2 **a)** Mean species endemic to the Wallacea hotspot detected per site in primary
838 forest, regenerating forest, disturbed secondary forest and cleared farmland in the
839 Lambusango Forest, South-East Sulawesi, (Kruskal-Wallis $H = 2.112$, $p = 0.348$). **b)**
840 Mean species endemic to the Mesoamerican hotspot detected per site in deep core,
841 boundary core and buffer zone sites within Cusuco National Park, Honduras (Kruskal
842 –Wallis $H = 14.04$, $p < 0.05$). Error bars represent 95% confidence intervals.

843

844 Figure 3 - Sample-based rarefaction curves displaying number of individual birds
845 detected against **a)** number of endemic species detected in primary forest (1),
846 regenerating secondary forest (2), and disturbed secondary forest (3) within the
847 Lambusango forest reserve, South-East Sulawesi, and **b)** number of highland forest
848 species detected in deep core forest (1), boundary core forest (2) and buffer zone
849 forest (3) in Cusuco National Park, Honduras.

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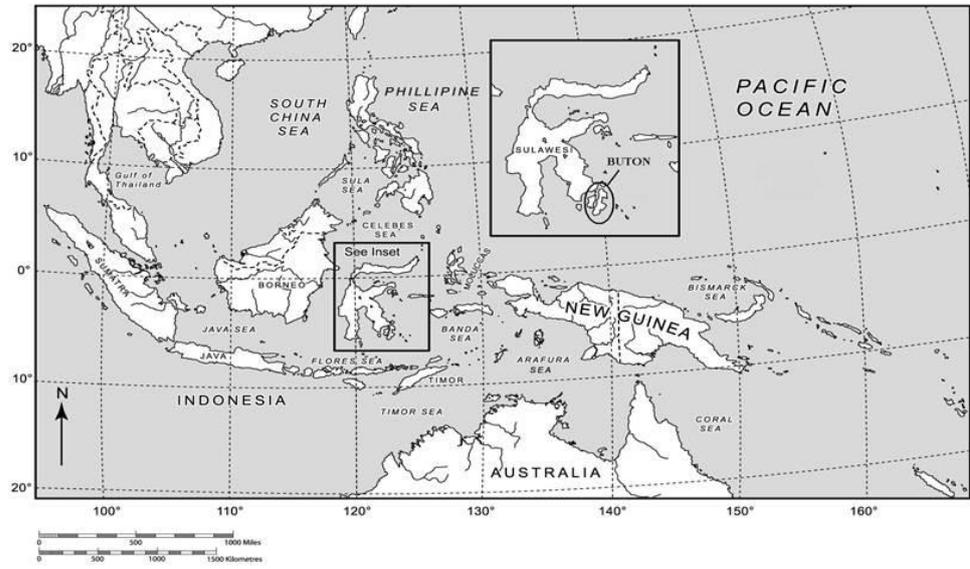
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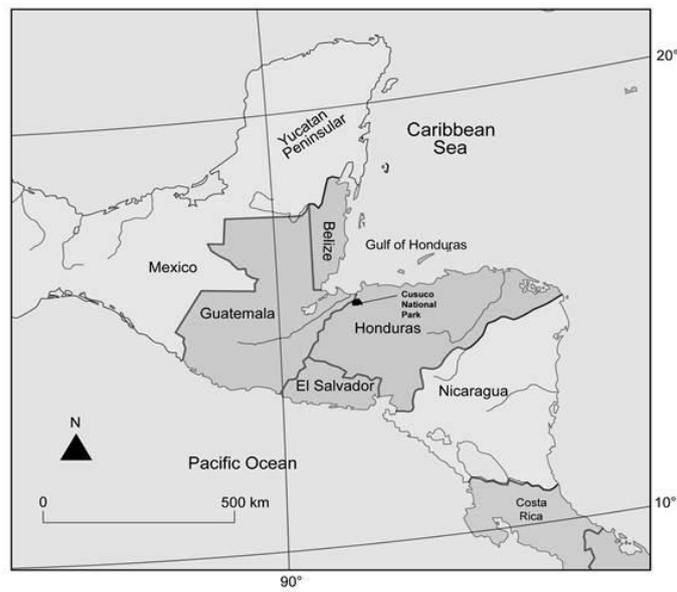
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A)



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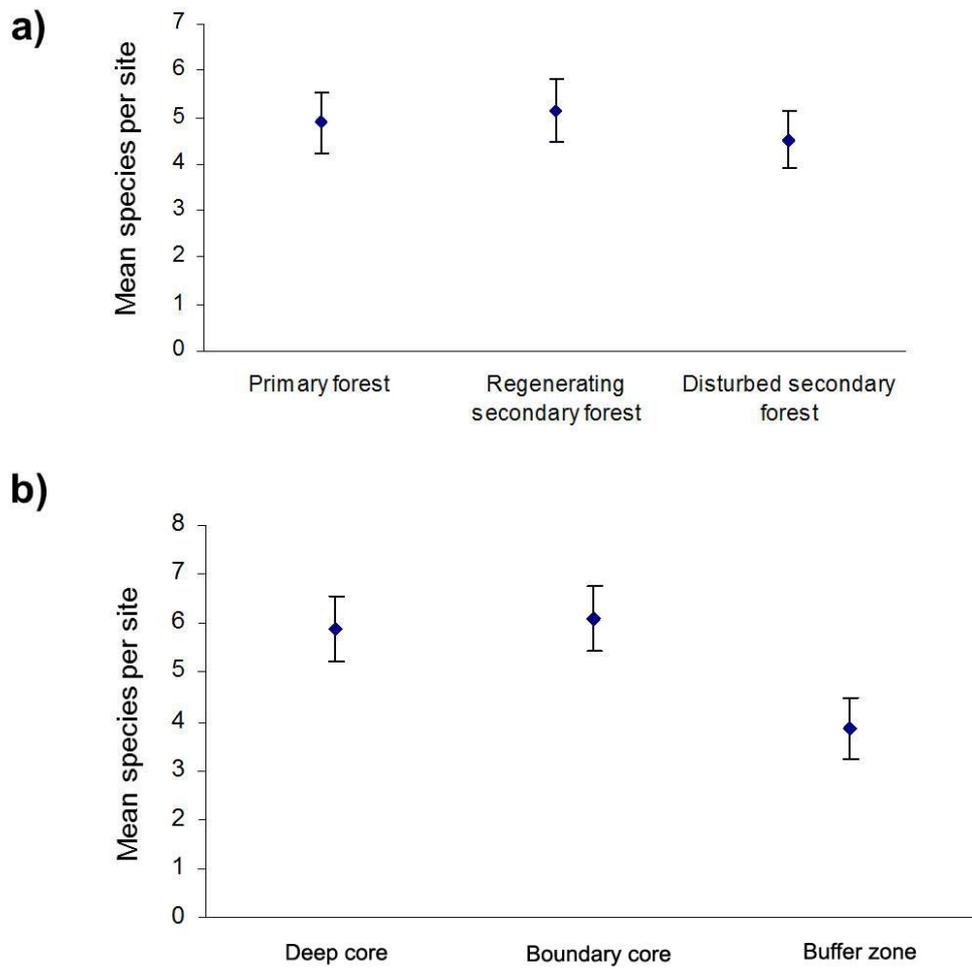
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859 Figure 1

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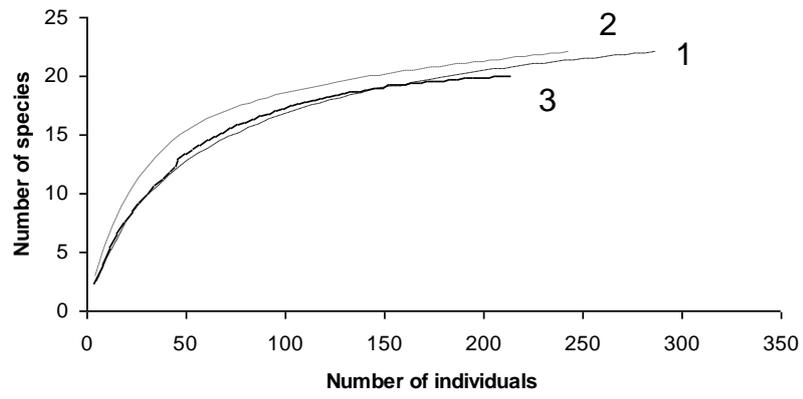
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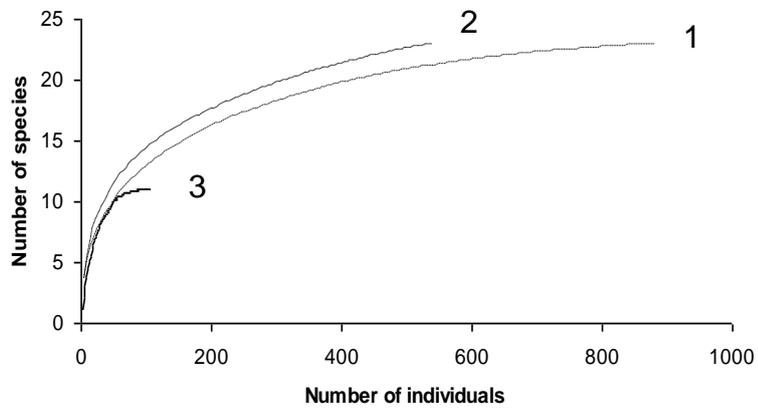
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878 Figure 3

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