1   **Conservation value of secondary forest habitats for endemic birds, a perspective**

2   **from two widely separated tropical ecosystems.**

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5   **Thomas Edward MARTIN[1]* George Alan BLACKBURN[1]**

6   **[1]Lancaster Environment Centre, Lancaster University, Lancaster, Lancashire,**

7   **UK. LA1 4YQ**

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9   *Corresponding author contact details:

10   tom_martin_2010@yahoo.co.uk

11   Tel: +44 1524 510237

12   Fax: +44 1524 510269

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

Key words: Avifauna; Biogeography; Endemism; Extinction; Mesoamerica; Wallacea

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INTRODUCTION

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

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

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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

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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.

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110   **METHODS**

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112   **<u>Study sites</u>**

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).

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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).

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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.

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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.

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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

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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).

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192   **<u>Bird sampling</u>**

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   detectibility 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.

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205   **<u>Vegetation surveys</u>**

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.

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225 **<u>Statistical analysis</u>**

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).

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236 **RESULTS**

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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 >30cm 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.

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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).

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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.

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287   **DISCUSSION**

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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

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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.

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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

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347   ecological and biogeographical factors could contribute to these apparent differences

348   in ecological vulnerabilities, which we consider below.

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350   **1 - Differential species richness**

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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

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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.

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

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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.

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

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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

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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 be 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

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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

19

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

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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**

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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

519   **ACKNOWLEDGEMENTS**

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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).*

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

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Table 2 - Vegetation variables in a) primary forest, regenerating secondary forest and disturbed

secondary forest in the Lambusango Forest Reserve, South East Sulawesi, and b) deep core, boundary

core and buffer zone sites in Cusuco National Park, Honduras. ± indicates variance to 1 standard

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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Table 3 - Non-parametric species estimators for a) primary forest, regenerating secondary forest,

disturbed secondary forest and cleared agricultural land within the Lambusango forest reserve, Buton

Island, South-East Sulawesi, and b) deep core, boundary core and buffer zone sites within Cusuco

National Park, Honduras. n represents sample size. Sp obs and Ind obs represent total number of

species and individuals observed, respectively. ACE, ICE, CHAO1, CHAO2, Jack1, Jack2, Bootstrap,

MMRuns and MMMeans are non-parametric species estimators (Colwell and Coddington, 1994).

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**

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).*

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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 *et al*. 2002
New Guinea	>50,000	O' Connell & Allen 2003
Sulawesi	> 30,000	Whitten *et al*. 2002
Lesser Antilles	5,000	Keegan & Diamond 1987
Madagascar	2000	Burney *et al.* 1997
Hawaii	1400	Keegan & Diamond 1987
New Zealand	800	McGlone 1989
Mascarenes	400	Keegan & Diamond 1987

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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.

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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

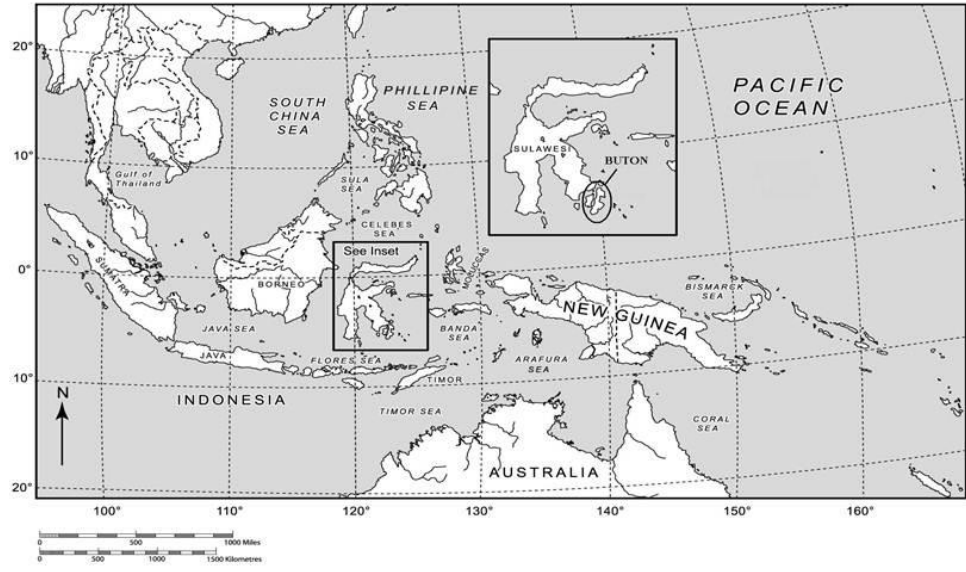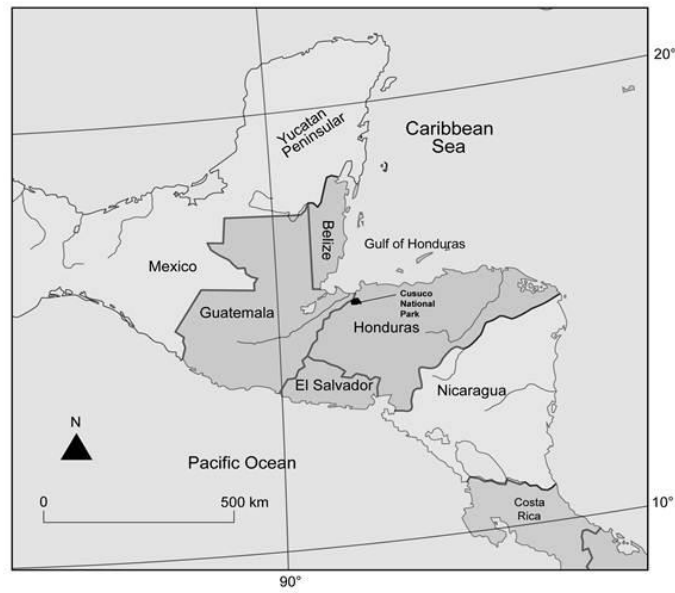849 forest (3) in Cusuco National Park, Honduras.
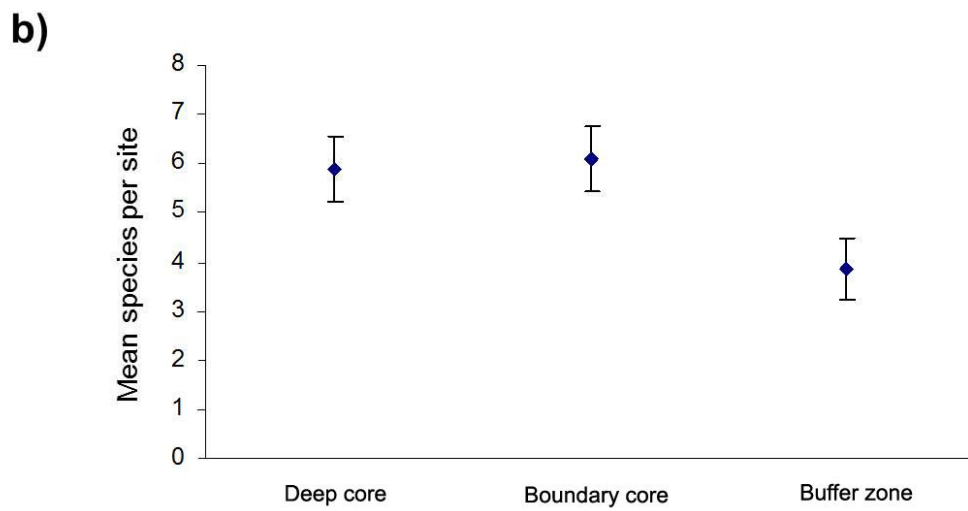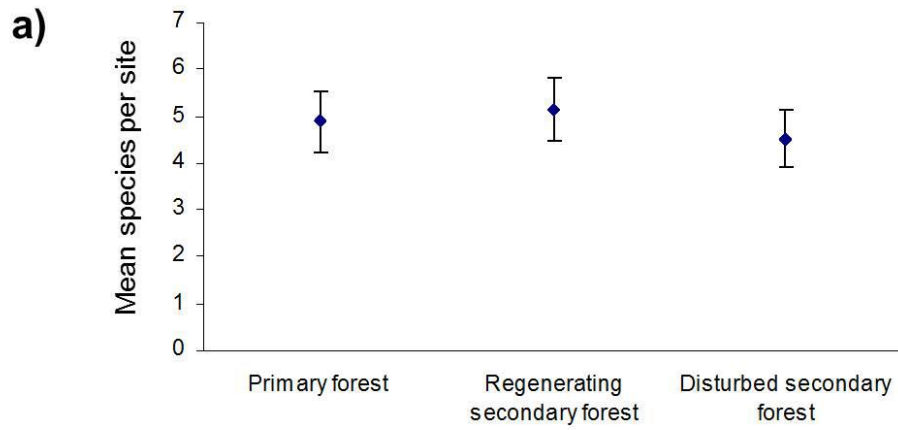
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A)

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859 Figure 1

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a)

Mean species per site vs forest type (Primary forest, Regenerating secondary forest, Disturbed secondary forest)

b)

Mean species per site vs zone (Deep core, Boundary core, Buffer zone)

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867   Figure 2

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Figure 3