1   **Contribution of agroforestry systems to sustaining biodiversity in fragmented forest landscapes**

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13

14 **Abstract**

15 Agroforestry systems maintain intermediate levels of biodiversity between natural forests and

16 purely agricultural land-uses and may therefore increase connectivity or sustain biodiversity in

17 fragmented forest landscapes. This hypothesis is tested by comparing the species richness and

18 similarity in species composition between forest fragments and agroforestry systems in two

19 landscapes in Guatemala. Connectivity indices were calculated based on the similarity of biodiversity

20 held between forest and agroforestry. Tree and ant species richness was significantly higher for

21 forest than agroforestry land-uses. Conversely, species richness of leaf hoppers (Cicadellidae) was

22 lower in forests compared to agroforests. Chao-Sorensen estimates indicated a high proportion of

23 ant species were shared (0.78-0.99) between different agroforestry land-uses and forest fragments,

24 but lower proportions of tree (0.39 – 0.55) and leaf hopper species (0.42-0.65). Including the

25 contribution of agroforestry systems in estimates of forest connectivity, based on their biodiversity

26 relative to forest, substantially increased the land area rated with high connectivity (by 100-300%)

27 and forest edge connectivity (by 70-170%), but had negligible impact on land area rated as dense

28 forest. The major forest fragments in the two landscapes were linked by land rated as medium

29 connectivity for forest biodiversity. Thus, agroforestry contributes to the capacity of the landscape

30 to support biodiversity, but only partially increases connectivity between forest fragments in the two

31 landscapes studied. If these benefits are to be sustained, consideration needs to be given to the

32 incentives for land-owners to maintain agroforestry systems.

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1. Introduction

Faced with the current threats to biodiversity such as climate change, invasive species, deforestation, and disruption of migration paths by infrastructure and human settlements, protected areas are insufficient to preserve biodiversity (DeFries et al. 2005; Millennium Ecosystem Assessment 2005). Therefore, agroecosystems need to play a complementary role to protected areas in the conservation of biodiversity (Vandermeer and Perfecto 2007; Harvey et al. 2008). The combination of crops with diverse tree assemblages in agroforestry systems have been found to maintain high levels of both flora and fauna (Tscharntke et al. 2011). Agroforestry has the potential to contribute to biodiversity conservation by creating habitat for species which are tolerant to some level of disturbance (Harvey and Villalobos, 2007). Agroforestry systems have therefore been proposed for use in buffer zones or biological corridors, as habitats for such species (Donald 2004; Mas and Dietsch 2004).

Agroforestry systems sustain higher biodiversity than agricultural systems through having greater plant diversity (including native species), increased structural complexity, and enhanced habitat and landscape heterogeneity. Tree species richness has been found to have close correlation with the diversity of fruit and nectar-feeding birds and fruit-feeding butterflies (Schulze et al. 2004) and with the diversity of arthropod groups such as ants (Leal et al. 2012). There have been numerous studies on different taxonomic groups in coffee agroforestry (often called shaded coffee) including migratory birds (Bakermans et al. 2009), orchids (Solis-Montero et al. 2005), bats (Estrada et al. 2006), ants (Armbrecht et al. 2005), and amphibians (Santos-Barrera et al. 2011), showing the potential for this system to conserving these species. The nature of the shade in coffee (and similar crops like cocoa or cardamom) varies considerably from heavily managed single species shade to highly diverse tree species assemblages (Moguel and Toledo 1999). In a metanalysis of studies comparing the relative biodiversity of forest, and coffee and cocoa agroforestry and monocultures, Beenhouwer et al (2013) found species richness to be 11% lower in agroforestry systems but 46% lower in monocultures

64 compared to forests. Nevertheless, the response of particular taxonomic groups can vary. For

65 example, compared to forest, Chandler et al (2013) found that compared to forest shaded coffee had

66 higher species richness of Nearctic migrant birds, but lower species richness of forest-dependent

67 species.

68   There is conflicting evidence as to whether there is a trade-off between crop productivity of

69 agroforestry systems and their potential to sustain biodiversity. Clough et al. (2011) observed no

70 relationship between yield and biodiversity in cocoa agroforestry systems in Indonesia. Haggar et al.

71 (2013 & 2017) in Guatemala and Nicaragua found that coffee had lower productivity on high shade-

72 tree diversity farms. Jezeer et al. (2017) in a meta-analysis of effects of shade concluded that while

73 productivity of shaded coffee may be lower, net income for the coffee grower was not significantly

74 different from unshaded coffee monocultures. Another consideration in the trade-off between

75 productivity and biodiversity is that to meet a certain global demand for coffee would require a greater

76 area of shaded coffee than unshaded coffee, and thus potentially spare less land for forest. Chandler

77 et al. (2013) in Costa Rica observed greater bird diversity on farms that were half unshaded coffee and

78 half forest, compared to farms that were 100% shaded coffee.

79   There is a significant overlap between major coffee production areas and biodiversity hot

80 spots (Myers et al 2000; Hardner and Rice 2002), such as in Mesoamerica, the Andean region and

81 southern India. A review of coffee shade systems (Jha et al 2014) indicates that at least 80% of

82 coffee in these regions is shade-grown; 20-40% of this area with at least 10 tree species and over

83 40% shade cover that would be expected to maintain high biodiversity. Some studies have

84 documented the replacement of shaded coffee with other land-uses presumed to be less favourable

85 to biodiversity (Bosselmann et al 2012, Haggar et al 2013). In some countries such as El Salvador

86 where little natural forest cover exists, 80-92% of "forest" cover is estimated to consist of tree cover

87 from shade-grown coffee (Rice and Ward 1996). Moguel and Toledo (1999) concluded that coffee

88 plantations in Mexico could serve as important corridors for flora and fauna.

89   Agroforestry systems have been widely considered to maintain biodiversity in former forest

90   landscapes, provide corridors between forest patches, or act a buffer zones around protected forest

91   areas (Harvey et al 2008, Bhagwat et al 2008, Tscharntke et al 2011). Tree plantation systems may

92   be expected to also have similar benefits, but comparisons with agroforestry are lacking. If

93   agroforestry or tree-cropping systems are to be promoted buffer zones or corridors around

94   protected areas, clearer evidence is required regarding their potential to increase the biodiversity of

95   landscapes and the connectivity between forest fragments. Evidence of the role of agroforestry and

96   tree-crop production systems in sustaining biodiversity in two fragmented forest landscapes in

97   Guatemala was sought to answer the following questions:

98   • What is the species richness hosted by agroforestry systems compared to natural forest?

99   • What is the degree of similarity in species composition of agroforestry compared to forest

100   biodiversity?

101   • What is the contribution of agroforestry systems to estimates of connectivity for forest

102   biodiversity in the landscape?

103

104   **2. Methods**

105   *2.1 Country and site description*

106   Guatemala has been recognized as a "Megadiverse" country under the Convention on

107   Biological Diversity (http://paisesmegadiversos.org/en/). While 34% of the country is forested most

108   of this is in high montane zones or the lowlands of Petén (CONAP 2009). Little natural forest cover,

109   and few protected areas are found in the mid-altitude zones (500-1500 m.a.s.l.) where shaded

110   coffee and other agroforestry systems are common. The current study was conducted in two such

111   landscapes. One site, on the southern slope of the Pacific volcanic chain, is dominated by coffee

112   agroforestry and has probably been converted from forest over a century ago. Recent studies show

113   coffee agroforests have been replaced by other tree crops, such as rubber and macadamia,

114   generating concern regarding possible environmental impacts (Haggar et al 2013). Within this region

115   the Palajunoj landscape of northern Retahuleu, southern Quetzaltenango and eastern Coatepeque

116   was chosen because previous research with local land owners had been conducted there. Altitude

117   ranged from 440–1440 m.a.s.l. with annual rainfall about 3000 mm and a four-month dry season.

118   This study landscape covers approximately 267km^2. The other landscape was in eastern Guatemala,

119   on the southern slope of the Polochic Valley, part of the buffer zone of the Sierra de las Minas

120   Biosphere Reserve. This region was largely converted from forest within the past 20-30 years,

121   dominated by shifting cultivation with some presence of coffee and cardamom agroforestry. The

122   Biosphere Reserve management aims to understand whether promotion of agroforestry will help

123   improve the biodiversity status of the buffer zone. Within this greater region the study landscape

124   focused on the municipalities of La Tinta and Panzos of Alta Verapaz Department because

125   collaboration between the local indigenous communities and the project partner, the Fundación

126   Defensores de la Naturaleza, had already been established. Altitude ranged from 723-1377 m.a.s.l.

127   with annual rainfall about 2500 mm, only a two-month dry season. This study landscape covers an

128   area of approximately 116 km^2.

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130   *2.2 Selection of land-uses*

131   In each landscape the main tree plantation or agroforestry systems that may contribute to

132   biodiversity connectivity were identified based on past research (Haggar et al 2013), and

133   reconnaissance with local partners. We followed the established definition of agroforestry (Nair

134   1993) that includes traditional shifting cultivation where the fallow phase develops woody regrowth

135   as an agroforestry system. Based on previous research in Palajunoj, we differentiated shaded coffee

136   into "Agroforest Coffee", containing a mixture of native timber trees and planted legumes (usually

137   *Inga* spp.), and the simpler "Inga-shaded coffee" with only planted legume trees (Haggar et al 2013).

138   The main tree crops included in this study were rubber below 800 m.a.s.l. and macadamia at higher

139   altitudes, previous research showing they were the tree crops being planted to replace coffee. The

140   aim was to sample the different land-uses under similar conditions. Therefore, sampling was done

141   on the same estates (Palajunoj) or communities (Sierra de las Minas) in as close proximity as possible

142   (Table 1).

143

144   *2.3 Evaluation of biodiversity in different land-uses*

145   The use of different taxa to describe the biodiversity of an area was studied by Kessler *et al*.

146   (2011). They found correlations between bryophyte, pteridophyte, tree, ant, euglossine bee, bird,

147   spider and beetle species richness and concluded that only four taxa are required to represent at

148   least 80% of variation in species richness, while trees and ants alone would explain 60% of this

149   variation. We therefore selected trees and ants as the primary biodiversity indicator groups,

150   complemented by Cicadellidae (leaf hoppers) that may be expected to respond in a distinct manner

151   to the other two groups. Measuring the diversity of arthropods in litter is a commonly used method

152   for assessing the species richness and abundance of arthropods and about 60% of neotropical ants

153   are found in litter (Longino *et al.* 2002).

154   Sample plots were taken in one field of each land-use in each estate or community. Sample

155   plots measured 25 x 40 m in Palajunoj and 25 x 10 m in Sierra Las Minas. Differences in sample plot

156   sizes were due to the different tree densities and field dimensions, with much smaller fields in Sierra

157   Las Minas (<0.5 ha) often aligned across the slope. In other respects, the sampling was the same,

158   with all trees over 5 cm diameter at breast height measured within the plot.

159   Ants were sampled from three 1m^2 quadrats of leaf litter taken 10 m apart on a transect

160   across the sample plot. Samples were combined and left in a mini-Winkler sack for 48 hours

161   following the "Ants of leaf-litter" protocol (Longino, et al. 2002). Cicadellidae were sampled by

162   sweeping the herbaceous vegetation with 20 sweeps of a net through the top of the vegetation at

163   each sub-sampling point. The contents of the net were then passed into a flask with ethanol.

164   Although less effective than fumigating, sweeping still produces reliable relative data and is more

165   practical and efficient to apply under field conditions (Lowman and Wittman 1996). Trees, ants and

166   Cicadellidae were identified to species where possible and otherwise morpho-species were

167 differentiated. Reference collections of arthropod species were deposited in the collection of the

168 University of Valle Guatemala. The most common species in each taxonomic group are presented in

169 the Appendix (Tables B.1, B.2 and B.3).

170 *2.4 Analysis of species richness, diversity and similarity*

171 Sample-level plot data were tested for normality using the Shapiro Wilk test and residuals

172 plotted. In general, the species richness values were not normally distributed and were therefore

173 analysed using a generalized linear model with Poisson distribution. The Shannon Diversity Index

174 values followed a normal distribution and were analysed using ANOVA. In both cases Tukey tests

175 were applied to compare between different land-uses. Effects of land-use on species composition

176 were assessed by Non-metric Dimensional Scaling (NMDS) analysis using the Adonis function in the

177 Vegan package of "R". The proportion of forest species shared by the other land-uses and the

178 similarity in composition were calculated using the EstimateS programme (Colwell 2013, Colwell et al

179 2012). Three different metrics were calculated:

180   i. Percentage of species shared between forest and other land-uses.

181   ii. Chao-Sorensen estimate of proportion of species in common between land-uses, including

182   estimates for unseen species (i.e. rare species) that were not found in the sampling plus an

183   estimated SD for this proportion (Chao et al 2006).

184   iii. Morisita-Horn index of similarity in species composition based on the relative abundance

185   of species between land-uses.

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187 *2.5 Land-use mapping and connectivity*

188 Land-use maps were obtained from classifications of Rapid Eye satellite images from the

189 year 2012 (Appendix Fig. D1 a & b) and total area under each land use was calculated (Appendix A,

190 table A.1). We used automated methods to differentiate land-use classes from classified field

191 observations. The resulting land-use maps were then verified by ground truthing a selection of

192   points in the field. Unfortunately, it was not possible to differentiate Agroforest coffee from Inga-

193   shaded coffee in the Palajunoj region.

194   Spatial statistics were used to calculate the degree of forest isolation or connectedness of

195   each pixel by analysing forest cover of surrounding pixels (Sastre and de Lucio 2002). In Rapid Eye

196   images each pixel is 5 meters across, the patch for which connectivity was calculated was a 1 x 1 km

197   square consisting of 200 by 200 pixels. Each pixel was scored as 1 if with forest and as 0 with any

198   other land-use. The sum of the scores of the surrounding pixels gives the degree of connectedness of

199   the central pixel to the forest. The spatial statistics analysis conducted using Focal Statistics (ESRI

200   2011) gives the relative connectivity in a range of 0 (no forest pixels in the 1 km square around the

201   central pixel) to 40 (all pixels in the 1 km square are forest). Connectivity values were reclassified

202   into six equal ranges and transformed from the 0-40 scale into a 0-1.0 connectivity index (Appendix

203   A Table A.2). The sum of the scores of all pixels across the landscape was used to calculate overall

204   index of connectivity for the landscape (Baskent and Jordan 1995). These ranges were determined

205   in accordance with a previous study by the National Institute of Forests of Guatemala "Identification

206   and Prioritization of Forest Corridors in Guatemala" (Anzueto and Pérez 2005).

207   As recognized by Fortin et al (2012), connectivity analyses need to consider the quality of the

208   intervening landscape between habitat patches. In our case these were the agroforestry and tree

209   plantation systems between the forest fragments. They have been integrated into the estimates of

210   connectivity based on the similarity of the biodiversity held compared to forest. The Morisita-Horn

211   index of similarity was used as it combines the similarity of observed species with the relative

212   abundance of those species between the forest and other land-uses. The Morisita-Horn diversity

213   index was averaged across the three taxonomic groups (plants, ants, and Cicadellidae) to give an

214   overall estimate of the similarity of biodiversity between the different land-uses and the forest

215   (Appendix A, table A.3). In the estimates of connectivity, pixels with agroforestry or tree plantations

216   were scored according to their average Morisita-Horn index (e.g. fallow = 0.509). Land-uses without

217   trees was assumed to have zero forest biodiversity. While assuredly this is a simplification, the same

218   assumption is made in the original forest connectivity calculation. For each landscape different

219   connectivity scenarios were generated adding one by one each agroforestry or tree plantation land-

220   use to the analysis. Land-uses were added to the connectivity scenarios and maps in order of

221   descending Morisita-Horn index. The change in overall connectivity index and area of land with

222   different degrees of connectivity with forest were calculated for the addition of each land-use.

223

224   **3. Results**

225   *3.1 Species richness and diversity*

226   3.1.1 Trees

227   Tree species richness was significantly different between land-uses in Palajunoj ($F=19.35$

228   DF=19, $p<0.0001$). Forest had significantly greater species richness than other land-uses ($p<0.001$),

229   while the other land-uses had similar species richness except the Agroforest coffee which had a

230   significantly greater species richness than the other non-forest land-uses ($p<0.05$; Fig. 1a & b).

231   Shannon Diversity Index was significantly affected by land-use ($F=21.15$, DF=26, $p<0.0001$). Forest

232   had a higher Shannon Diversity ($p<0.05$) compared to other land-uses except the agroforest coffee.

233   Inga coffee had a greater tree diversity ($p<0.05$) than rubber plantations. In Sierra de las Minas land-

234   use significantly affected tree species richness ($F=28.98$, DF=26, $p<0.001$) and Shannon Diversity

235   Index ($F=15.73$, DF=26, $p<0.001$); both were significantly greater ($p<0.001$) for the forest compared

236   with the rest of the land-uses (Fig. 1c & d). Adonis analysis of tree species composition found a

237   significant effect of land-use in both Palajunoj ($F=6.93$, DF=35, $p<0.001$) and Sierra Las Minas

238   ($F=2.17$, DF=29, $p<0.001$; NDMS graphs are shown in appendix C.1).

239   3.1.2 Cicadellidae

240   In both landscapes and both seasons Cicadellidae species richness was significantly affected

241   by land-use (Palajunoj dry season $F=3.36$, DF=25, $p<0.05$; wet season $F=4.49$, DF=25, $p<0.05$; Sierra

242   Las Minas dry season $F=2.68$, DF=26, $p=0.54$, wet season $F=5.88$, DF=26, $p<0.01$), and was always

243   lowest in the forest. In Palajunoj, compared to forest, species richness was significantly higher in

244   macadamia plantations in the dry season ($p<0.05$; Fig. 2 a). In Sierra Las Minas, compared to forest,

245   species richness was significantly higher in coffee and fallow in the wet season ($p<0.05$; Fig. 2 b).

246   Shannon Diversity Index was significantly lower in forest than most other land-uses in the wet

247   season in both Palajunoj (forest 0.51 vs 1.09 - 1.44 for other land uses, $p<0.05$) and Sierra Las Minas

248   (forest 0.9 vs 2.9 - 6.3 for other land-uses, $p<0.05$); but there was no significant differences in the dry

249   season. Adonis analysis revealed no significant effect of land-use on species composition for either

250   landscapes (NMDS graphs are shown Appendix C.2).

251   3.1.3 Ants

252   Overall there was no significant effect of land-use on ant species richness in Palajunoj,

253   although individual comparisons of means indicated significantly higher ($p<0.05$) species richness in

254   the forest than rubber in Palajunoj in the wet season (Fig 3a). In Sierra las Minas land-use

255   significantly affected species richness both in the wet season ($F=4.32$, $DF=26$, $p<0.05$) and dry season

256   ($F=9.0-$ $DF=24$, $p<0.001$); forest had significantly higher species richness ($p<0.05$) than fallow in both

257   seasons and coffee in the dry season (Fig. 3b). Shannon Diversity Indices were not significantly

258   different between land-uses. Ant species richness was positively correlated with tree species

259   richness (0.49, $p<0.001$) in Sierra las Minas but not in Palajunoj. Adonis analysis of species

260   composition found significant effects of land-use in both Palajunoj ($F=1.54$, $DF=35$, $p<0.01$) and

261   Sierra Las Minas ($F=1.32$, $DF=35$, $p=0.079$; NDMS graphs are shown in appendix C.3).

262

263   *3.2 Species composition compared to forest*

264   3.2.1 Palajunoj

265   In terms of tree diversity, samples from the two coffee systems shared a third of the forest

266   species, but when considering inclusion of rare species using the Chao-Sorensen index, 55% of

267   potential species are estimated to be shared (Table 2). Both indices are lower in rubber and

268   macadamia when compared to forest. The Morisita-Horn index, that gives more weight to the

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269   relative abundance of species, indicates that agroforest coffee had the greatest similarity to the

270   forest, and rubber plantations had the least similarity.

271   For ants the percentage of species sampled that are shared with the forest ranged from 63%

272   for macadamia to 70% for Inga coffee. The Chao-Sorensen estimate of potential shared species with

273   forest was between 85% (macadamia) to nearly 100% (Inga coffee). Rubber plantations were

274   estimated to share 98% of species with the forest. The Morisita-Horn index of similarity to forest was

275   lowest for Inga coffee and highest for agroforest coffee and rubber, although the range in values

276   across systems was small. Overall, this indicated that most ant species were probably shared

277   between all land-uses and the relative abundance was similar. The effects were similar for

278   Cicadellidae with the main difference being that the forest had fewer species than the other land-

279   uses; the majority of Cicadellidae species were however shared with the other land-uses.

280   Nevertheless, the coffee agroforest shares the most species with the forest and had a substantially

281   higher Morisita-Horn index of similarity in relative abundance.

282   3.2.2 Sierra de las Minas

283   In Sierra de las Minas (Table 3) sampled tree species that are shared with the forest varies

284   from 26% (coffee) to 20% (cardamom). The Chao-Sorensen index, that includes estimates for rare

285   species, however, estimates shared species with forest to be 39% for fallow and 46% for coffee. In

286   contrast the fallow had a considerably higher Morisita-Horn similarity to forest compared to coffee.

287   This may be because the shade trees in the coffee were dominated by planted *Inga* spp. and

288   *Gliricidia sepium*, which did not appear in the forest plots, although a selection of native trees

289   remained.

290   The cardamom, coffee and fallow land-uses shared about two-thirds of ant species with the

291   forest according to the sampling data, while the Chao-Sorensen index estimated over 90% of species

292   in coffee and fallow were shared with forest. In contrast the Morisita-Horn similarity index, that

293   takes into account abundance, indicates that cardamom was the most similar to the forest in ant

294   species composition.

295   Forests had an inferior Cicadellidae species richness compared to other land-uses. Coffee

296   and cardamom share 23-26% of the forest species sampled, while Chao-Sorensen index estimated

297   65% of species could be shared. Fallow shared only 17% of sampled species with forest, or 42%

298   according to Chao-Sorensen. The relative species abundance according to the Morisita-Horn index

299   was more similar between cardamom and forest than with other systems, but differences were

300   small.

301

302   *3.3 Connectivity for forest biodiversity*

303   When just considering forest cover, connectivity for forest biodiversity was restricted to the

304   bands of riverine forest running North-South along the major rivers in Palajunoj (Appendix Fig. D2).

305   The addition of the coffee agroforestry systems (scenario 2) substantially reduced the area with no

306   connectivity (Fig. 4a). This increased the area in medium connectivity (140% increase), high

307   connectivity (85% increase) and forest edge (65% increase), generating a "medium-level" East-West

308   connectivity between the riverine forest strips. In terms of overall forest biodiversity connectivity,

309   the coffee agroforestry system added 41% of the overall forest biodiversity connectivity, almost as

310   much as the forest itself (Table 4). The inclusion of the macadamia and rubber plantations led to

311   minimal improvements in connectivity, because macadamia was grown in a small area and rubber

312   plantations hosted less forest biodiversity.

313   For the Sierra Las Minas landscape when only forest was taken into account there was no

314   connection for forest biodiversity between the southern forest (Biosphere reserve core protected

315   area at lower edge of the map) and the small remnant forest patch in the mid-north (Appendix Fig.

316   D3). With the addition of fallow, the area with high to edge forest level connectivity increased by

317   147% and 58% respectively. The addition of the cardamom agroforestry increased the area with

318   medium level connectivity, but only with the addition of coffee (which has a larger area) was a

319   medium level of connectivity fully established between the northern forest patch and southern

320   forest block. The area with "dense forest" connectivity for biodiversity was little changed with

13

321 addition of agroforestry land-uses. The area with no connectivity however declined substantially

322 while the area with medium and high connectivity for forest biodiversity increased by about three-

323 fold (Fig. 4b). Overall the fallow made a slightly larger contribution to the final connectivity index

324 than the forest itself due to the greater area under fallow (Table 4). The cardamom and coffee

325 agroforestry systems made smaller contributions to the connectivity index but were still important

326 for achieving a medium level of connectivity between the north and south forest patches.

327

328 **4. Discussion**

329 *4.1 Relative species diversity in agroforest and forest systems*

330 In the Palajunoj landscape there were significant differences in tree diversity between the

331 different land-uses, with the coffee systems being most similar to the forest. However, while the ant

332 species richness indicated a probable difference between rubber plantations and forests, the Chao-

333 Sorensen estimate of total ant species in common between forest and rubber indicated they shared

334 very similar species assemblages. While ant diversity has been considered a good indicator of overall

335 species diversity in tropical forest systems (Kessler et al 2011, Longino et al 2002), other studies

336 indicate that specialist primary forest ant species disappear quickly with any disturbance (Leal et al

337 2012). The forest patches in the study landscapes were highly fragmented, have been exploited for

338 timber, and in some cases are old secondary forest. Consequently, they may have already "lost" the

339 primary forest species and only host species that can survive in a disturbed landscape and are

340 therefore also adapted to the tree plantation and agroforestry systems. The alternative explanation

341 was that the actual sampled ant species richness may be a more reliable indicator than the Chao-

342 Sorensen estimate based on an extrapolated estimate of the rare species that might be shared.

343 In the Sierra de las Minas landscape there was also reason to believe that the different land-

344 uses largely draw upon the same pool of species. The Chao-Sorensen estimates over 90% ant species

345 were shared between forest and two of the three non-forest land-uses. The dimensions of the land-

346 use units in this landscape were much smaller than in Palajunoj (generally less than 0.5 ha in Sierra

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347 Las Minas; as opposed to 10s of ha in Palajunoj). There was also a temporal dynamic between

348 secondary forest or fallow converted to maize, coffee, or cardamom production and then

349 abandoned if productivity or prices fall. Nevertheless, despite being disturbed, the agroforestry

350 land-uses still maintained species associated with primary forest (e.g. trees *Magnolia guatemalensis*

351 and *Hedyosmum mexicanum*, and ants *Thaumatomyrmex ferox* and *Tatuidris tatusia*). Thus, the

352 mosaic of different land-uses maintained some forest species (as also indicated by the Chao-

353 Sorensen Index), but at different frequencies (as indicated by the Morisita-Horn index). The question

354 then remains whether these species were remnant individuals from the original forest (which might

355 be the case for the trees) or whether they represent viable populations (presumably the case for the

356 short-lived ant species).

357 　　　Beenhouwer et al (2013) reported that on average agroforestry systems supported 11%

358 fewer species than forest. The current study would suggest the degree to which forest and

359 agroforestry share species to vary considerably between taxonomic groups. The agroforestry

360 systems were estimated to share (Chao-Sorensen index) 39-55% of tree species, 42-65% of

361 Cicadellidae, and 78 - 99% of ant species with the forest. Furthermore, while species may be shared

362 between agroforestry and forest their relative abundance may be different as indicated by the low

363 Morisita-Horn similarity index of plant diversity relative to the number of shared species. In

364 particular, the lower proportion of shared tree species was due to the presence of planted locally

365 non-native tree species. This was similar to findings of Häger et al (2014) showing that while 73% of

366 tree species were naturally regenerated native species, 55% of individuals in coffee agroforestry

367 were non-native tree species.

368

369 *4.2 Role of agroforests for sustaining biodiversity in the landscape*

370 　　　The agroforestry systems (coffee, cardamom and fallow) made significant contributions to

371 the connectivity for forest biodiversity in the fragmented landscapes. Without these tree-based

372 systems, forest fragments were clearly isolated from each other (Palajunoj) or from larger forest

373   protected areas (Sierra de las Minas). Inclusion of the biodiversity hosting capacity of the

374   agroforestry systems substantially increased the biodiversity supporting capacity of the landscape

375   overall (increase in high connectivity and edge forest area by 70-100%) and consolidated or

376   expanded some forest fragments. Additionally, agroforestry systems also generated connectivity

377   between those forest fragments albeit only at a "moderate" level. As recognized previously,

378   agroforestry systems only host a portion of forest biodiversity (Beenhouwer et al 2013) and this

379   appeared to be reflected in the moderate level of connectivity for forest biodiversity observed in the

380   maps.

381   The effectiveness of agroforestry systems to support forest biodiversity appeared to rest on

382   the degree to which they incorporate native forest trees. Thus, in Palajunoj the agroforest coffee

383   generally had the highest number of estimated shared species (Chao-Sorensen index) and similarity

384   of relative abundance (Morisita-Horn Index) to the forest across the taxonomic groups.

385   Unfortunately, we were not able to differentiate agroforest and Inga-shaded coffee in the mapping

386   to evaluate their relative importance.

387   Studies, such as the current one, may be used to support conservation management

388   decisions. In Sierra de las Minas the Fundación Defensores de la Naturaleza who manage the

389   biosphere reserve were able to justify supporting local communities to apply for forestry subsidies to

390   establish more coffee agroforestry systems with native trees as these can generate some income

391   and potentially increase the connectivity for biodiversity in the buffer zone. In the Palajunoj region

392   several farms were private nature reserves and some conduct eco-tourism. There was interest from

393   the Ministry of Environment to develop a coffee biological corridor along the slope of the Pacific

394   volcanic chain that includes Palajunoj; the evidence of biodiversity connectivity provided by the

395   coffee agroforestry systems supports the validity of this proposal.

396   Nevertheless, as found in earlier studies in this region (e.g. Haggar et al 2013 & 2017) the

397   productivity and income from coffee agroforestry was lower than from more intensive production

398   systems. If landowners are expected to conserve agroforestry practices, then they need to receive

399   other benefits. Forestry subsidies or eco-tourism may play a role here. Another option is the

400   sustainable certification of the coffee production under international standards such as Rainforest

401   Alliance, Organic or Fairtrade. Haggar et al (2017), found that farms under these schemes generally

402   had better environmental performance, and in some cases (principally organic farmers) higher

403   shade-tree diversity in the coffee plantations. Farmers of such certified systems also received

404   significantly higher prices for their coffee, although this does not always translate to increased net

405   income.

406   In summary, we have demonstrated that agroforestry systems improve forest biodiversity

407   connectivity as has been proposed (Harvey et al 2008). Although, connectivity may only be at a

408   moderate level across areas with only agroforestry and no forest fragments. If conservation

409   managers are to promote such approaches, then land owners will need financial support to develop

410   and maintain agroforestry systems where they may contribute to biodiversity connectivity.

411

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527

528   Table 1. Selected tree plantation or agroforestry land-uses and number of fields sampled for each

529   landscape

Palajunoj		Sierra Las Minas	
Land-use	Number of fields sampled	Land-use	Number of fields sampled
Forest	9	Forest	10
Agroforest Coffee	10	Fallow	10
Inga-shaded Coffee	10	Coffee	10
Rubber	6	Cardamom	10
Macadamia	5		

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531

Table 2. Tree, ant and Cicadellidae similarity in species composition between forest and other land uses in Palajunoj.

Taxa / Land use	Total number of species in land-use	Number of species in paired forest plots*	Shared species %	Chao-Sorense n	Estimated S.D.	Morisita-Horn
Trees						
Inga coffee Agroforest	45	89	32.8	0.548	0.11	0.076
coffee	53	89	35.2	0.554	0.109	0.183
Macadamia	32	64	22.9	0.334	0.140	0.068
Rubber	26	66	21.7	0.141	0.141	0.006
Ants						
Inga coffee Agroforest	53	55	70.4	0.997	0.022	0.610
coffee	45	55	68.0	0.929	0.042	0.704
Macadamia	44	48	63.0	0.846	0.066	0.672
Rubber	42	47	67.4	0.979	0.038	0.701
Cicadellidae						
Inga coffee Agroforest	28	28	46.4	0.753	0.076	0.298
coffee	42	28	60.0	0.986	0.044	0.604
Macadamia	42	25	53.7	0.861	0.073	0.283
Rubber	29	22	51.0	0.763	0.124	0.258

*The number of species in forest varies when compared with macadamia and rubber because the number of paired forest sites is smaller for these land-uses.

536

537 Table 3. Tree, ant and Cicadellidae similarity in species composition between forest and other land-

538 uses in Sierra de las Minas, Alta Verapaz, Guatemala.

Taxa/ Land use	Total number of species in land-use	Number of species in paired forest plots	Shared species %	Chao-Sorensen	Estimated S.D.	Morisita-Horn
Trees						
Coffee	31	86	25.6	0.462	0.144	0.222
Cardamom	22	86	20.4	0.442	0.142	0.322
Fallow	27	86	21.2	0.39	0.094	0.421
Ants						
Coffee	42	57	66.7	0.922	0.050	0.579
Cardamom	47	57	65.4	0.782	0.093	0.647
Fallow	52	57	71.6	0.97	0.021	0.617
Cicadellidae						
Coffee	34	10	22.7	0.657	0.22	0.482
Cardamom	21	10	25.8	0.656	0.17	0.553
Fallow	26	10	16.7	0.42	0.17	0.489

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543 Table 4. Comparison of increase in % of connectivity by scenario (for explanation see legend Figs. 4 a

544 & b)

	Sierra de las Minas			Palajunoj		
	Average connectivity index	Contribution to final estimate of connectivity		Average connectivity index	Contribution to final estimate of connectivity	
Scenario 1	0.17	Forest	35%	0.22	Forest	54%
Scenario 2	0.35	+Fallow	38%	0.39	+Coffee	41%
Scenario 3	0.41	+Cardamom	12%	0.39	+Macadamia	0%
Scenario 4	0.48	+Coffee	15%	0.41	+Rubber	5%

545

546

547   Figure Legends

548

549   Fig. 1 Tree species richness (a. in Palajunoj and c. Sierra Las Minas) and Shannon Diversity Index (b. in Palajunoj and d. in Sierra Las Minas) under different

550   land-uses in two landscapes in Guatemala. Columns that do not share the same letter are significantly different (p<0.05).
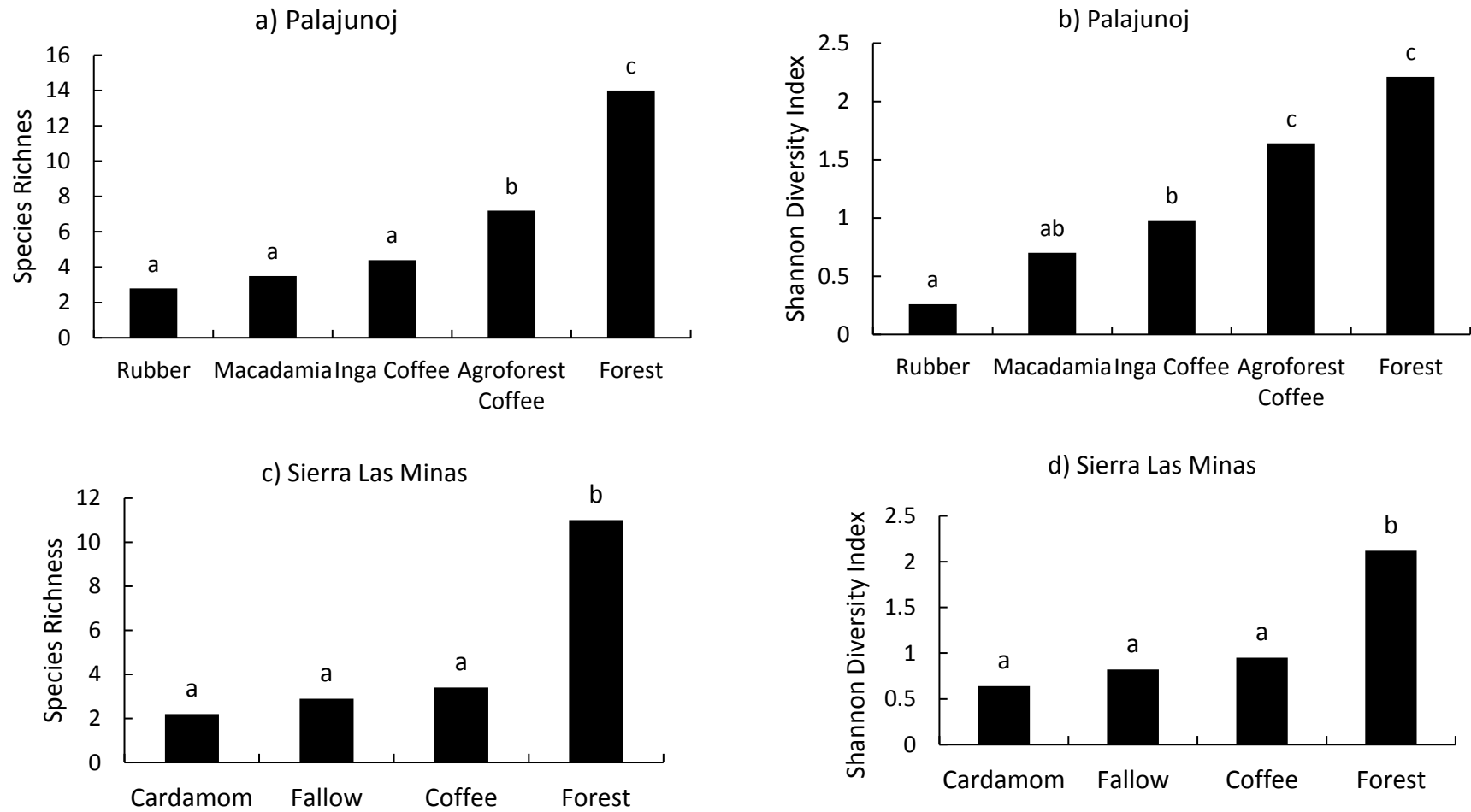
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552   Fig. 2 Cicadellidae species richness in wet and dry season under different land-uses in the two

553   landscapes: a) Palajunoj, b) Sierra Las Minas. Columns from the same season that do not share the

554   same letter are significantly different (p<0.05).

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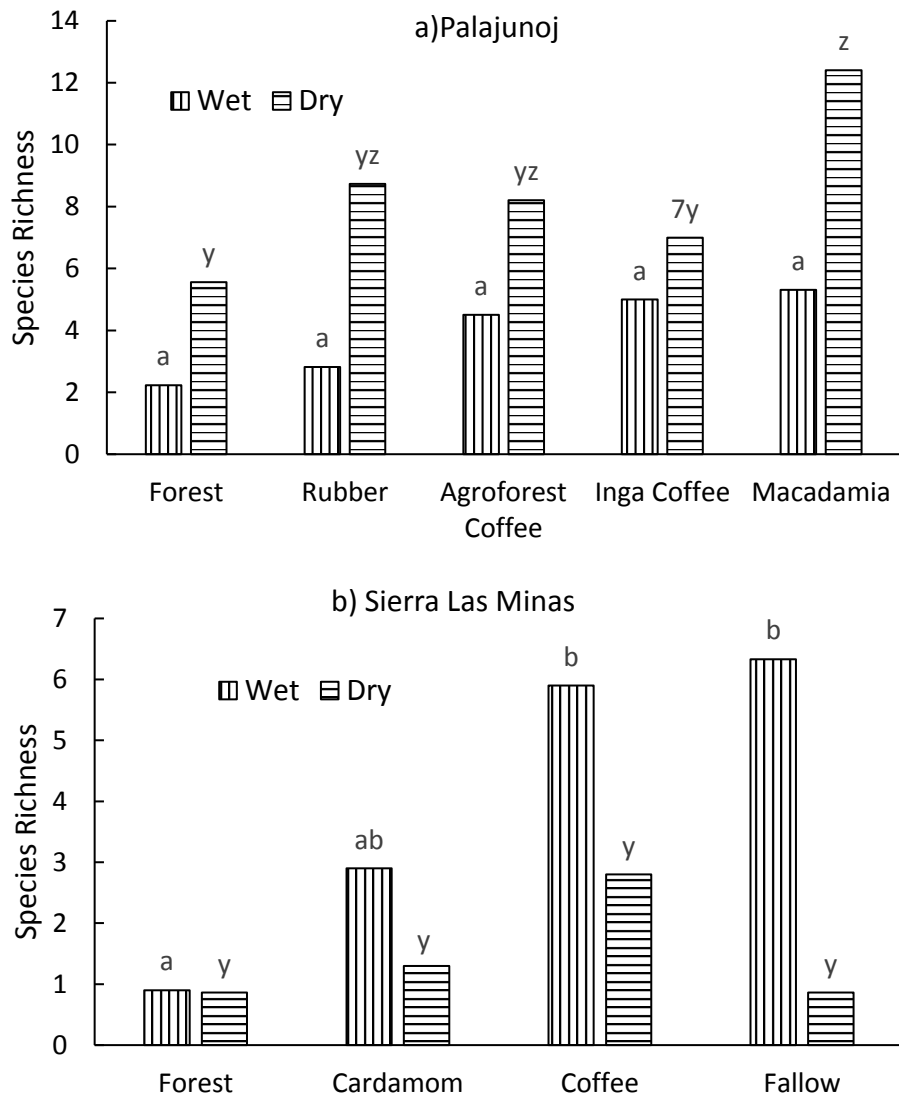
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559   Fig. 3 Ant species richness in wet and dry season under different land-uses in the two landscapes: a)

560   Palajunoj, b) Sierra Las Minas. Columns from the same season that do not share the same letter are

561   significantly different (p<0.05).

562
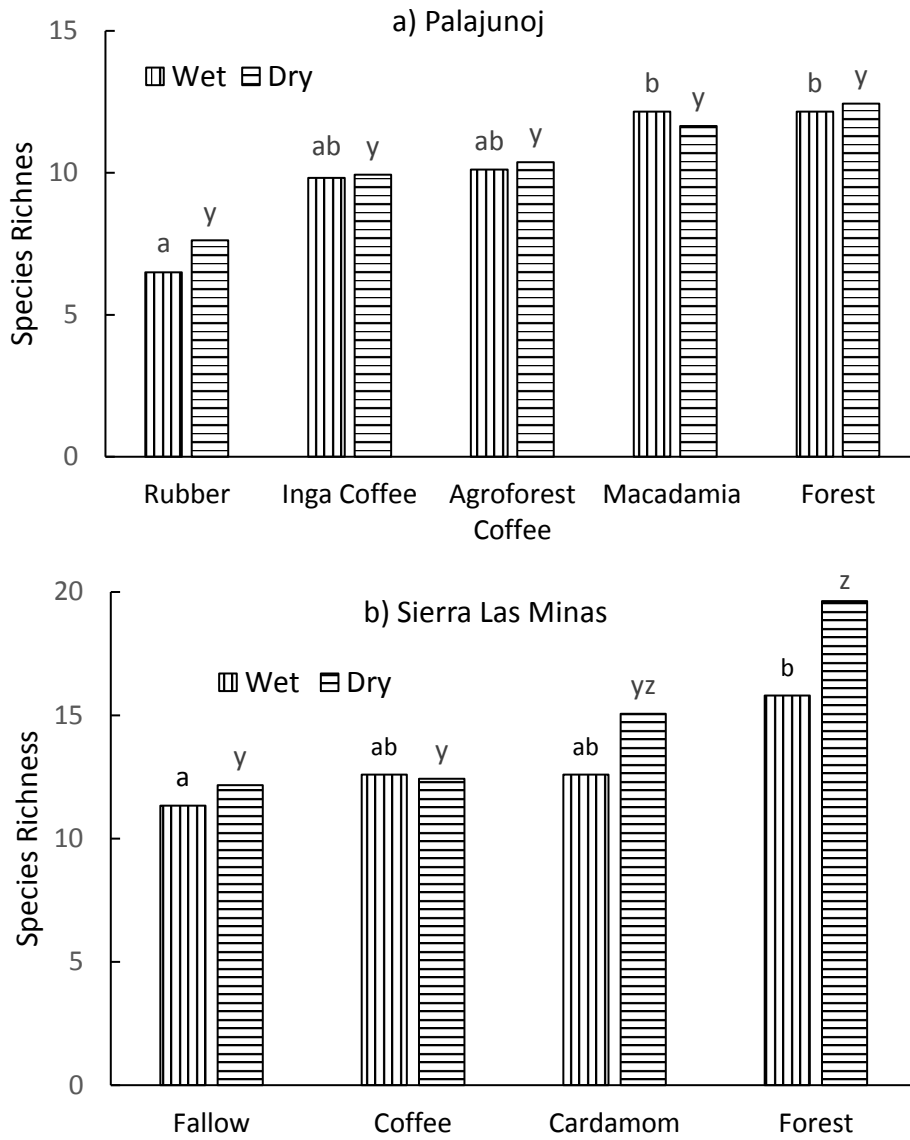
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567   Fig. 4. Area of land with different degrees of connectivity for forest biodiversity under the different

568   land-use scenarios: a) Palajunoj landscape (scenario 1 = forest, 2 = forest+coffee, 3 =

569   forest+coffee+macadamia, 4 = forest+coffee+macadamia+rubber; b) Sierra de las Minas landscape

570   (scenario 1 = forest, 2 = forest+fallow, 3 = forest+fallow+cardamom, 4 =

571   forest+fallow+cardamom+coffee).

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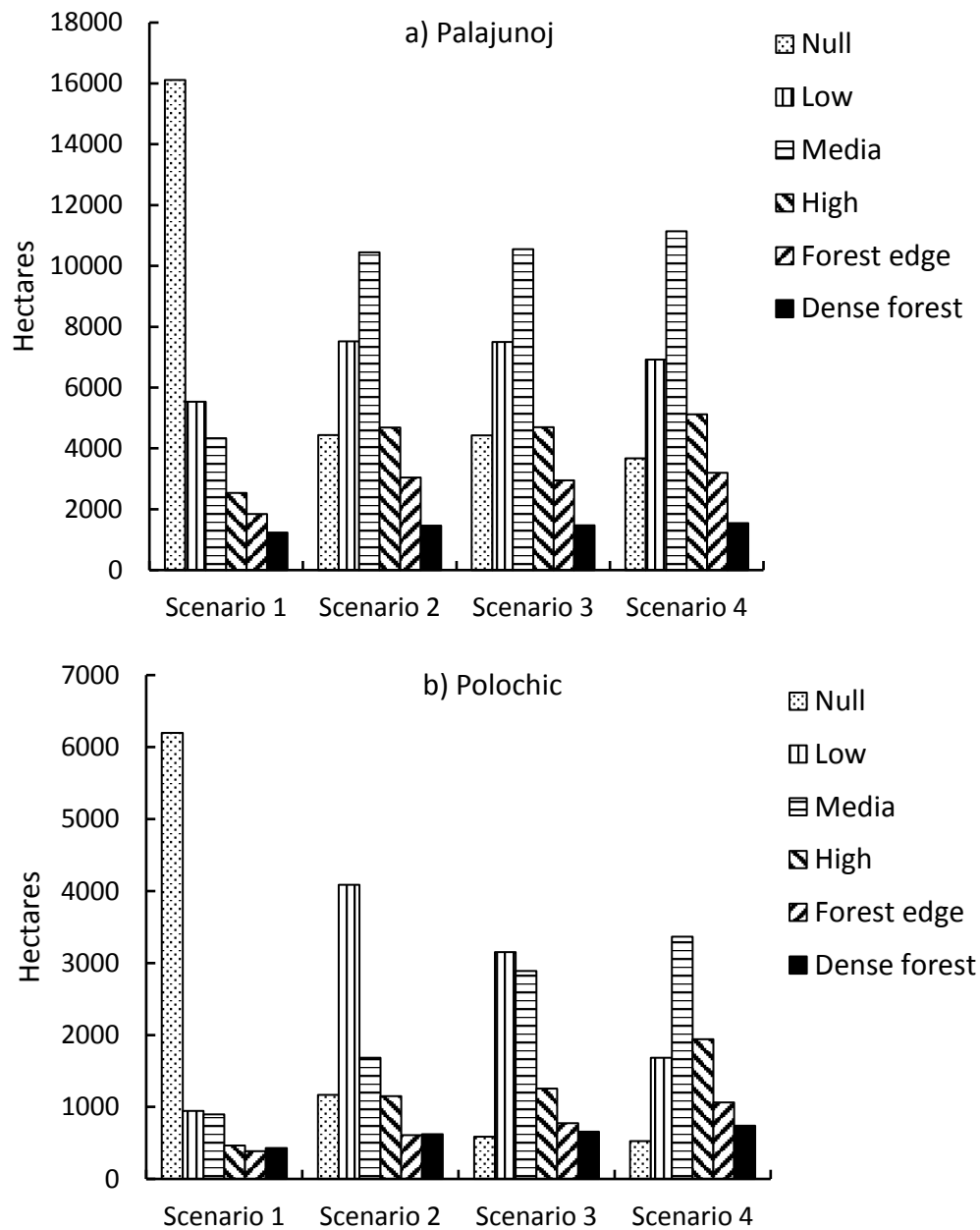
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Appendix A. Supporting metrics for estimation of connectivity

Table A.1. Area of major land-uses in each study landscape

Palajunoj			Sierra Las Minas		
Land-use	**Hectares**	**% area**	**Land-use**	**Hectares**	**% area**
Coffee	12,619	47.2	Fallow	5,167	44.6
Agriculture*	6,683	25.0	Forest	2,614	22.6
Forest	3,715	13.9	Coffee	1,882	16.2
Rubber	2,307	8.6	Agriculture*	968	8.4
Water bodies	679	2.5	Cardamom	890	7.7
Settlements	494	1.8	Rubber	50	0.4
Macadamia	235	0.9	Water bodies	19	0.2
Total	26,732		Total	11,590	

*treeless areas of herbaceous vegetation primarily either pasture or annual crops

Table A.2. Classification of connectivity ranges and connectivity index and classes assigned by range

Ranges	Connectivity index	Connectivity
0 - 6.5	0.0	Null
6.6 – 13.3	0.2	Low
13.4 – 20	0.4	Media
20 – 26.7	0.6	High
26.8 – 33.3	0.8	Forest edge
33.4 - 40	1.0	Dense forest

Table A.3. Composite index of similarity in species composition to forest for different land-uses based on Morisita-Horn similarity index averaged across the different taxonomic groups used to estimate relative contribution of different land-uses to forest biodiversity connectivity.

Sierra Las Minas		**Palajunoj**	
	Composite Biodiversity Index		Composite Biodiversity Index
Forest	1	Forest	1
Fallow	0.509	coffee	0.413
Cardamom	0.507	macadamia	0.341
Coffee	0.368	rubber	0.322
No forest	0	No forest	0

Appendix B. Most common species found in each land-use for each landscape.

Table B.1 Top five tree species. Total number of trees sampled is given in parenthesis. Where it was not possible to identify the scientific name of the species the local Que'chi name is given

a) Palajunoj – 94 tree species total

Forest (451)	Inga Coffee (194)	Agroforest coffee (228)	Rubber (202)	Macadamia (159)
Cecropia obtusifolia (49)	*Inga micheliana* (72)	*Ocotea effusa* (38)	*Hevea brasiliensis* (188)	*Macadamia integrifolia* (88)
Dendropanax arboreus (32)	*Inga vera* subsp. *spuria* (48)	*Terminalia oblonga* (37)	*Dendropanax arboreus* (5)	*Musa paradisiaca* (26)
Urera sp. (29)	*Inga punctata* (22)	*Inga micheliana* (36)	*Terminalia oblonga* (2)	*Inga vera* subsp. *spuria* (26)
Terminalia oblonga (27)	*Musa paradisiaca* (14)	*Dendropanax arboreus* (22)	*Musa paradisiaca* (1)	*Ocotea effusa* (5)
Chamaedorea sp. (24)	*Ocotea effusa* (4)	*Inga vera* subsp. *spuria* (15)	*Guarea glabra* (1)	*Terminalia oblonga* (5)

b) Sierra de las Minas – 86 tree species total

Forest (225)	Coffee (65)	Cardamom (58)	Fallow (56)
Micona sp. (21)	*Inga spuria* (11)	*Saurauia villosa* (17)	*Miconia* sp. (23)
Saurauia villosa (17)	*Gliricidia sepium* (10)	*Aegiphila monstrosa* (14)	Ch´ut (6)
Ficus sp. (12)	*Calophyllum brasiliense* (5)	*Swietenia macrophylla* (7)	Joow (5)
Hyeronima oblonga (10)	*Aegiphila monstrosa* (5)	*Inga edulis* (4)	Ch´eer (4)
Calophyllum brasiliense (9)	*Saurauia villosa* (4)	*Hevea brasiliensis* (4)	*Cercropia peltata* (3)

Table B.2. Most common ant species in each land-use in Guatemala. Number of individuals sampled is given after each name

a)   Palajunoj -84 species and morphospecies of ant in total

Forest		Inga-coffee		Agroforest Coffee		Rubber		Macadamia	
Pheidole harrisonfordi	414	W. auropunctata	883	P. harrisonfordi	779	Carebara urichi	635	P. harrisonfordi	585
Wasmannia auropunctata	325	Pheidole harrisonfordi	558	Wasmannia auropunctata	131	Pheidole harrisonfordi	211	Solenopsis geminata	272
Carebara urichi	320	Solenopsis geminata	311	Carebara urichi	115	Gnamptogenys strigata	67	Brachymyrmex sp.2	215
Octostruma balzani	272	Carebara urichi	222	Octostruma balzani	115	Octostruma balzani	55	Labidus coecus	187
Carebara intermedia	270	Acropyga exsanguis	150	Gnamptogenys strigata	96	Wasmannia auropunctata	53	Octostruma balzani	88
Strumigenys brevicornis	121	Brachymyrmex minutus	142	Hypoponera nitidula	72	Carebara intermedia	52	Brachymyrmex minutus	77
Strumigenys gundlachi	116	Octostruma balzani	81	Brachymyrmex minutus	49	Strumigenys elongata	48	Strumigenys gundlachi	61
Stenamma nonotch	98	Strumigenys elongata	57	Carebara intermedia	41	Brachymyrmex sp. 2	37	Strumigenys sp. 6	45
Hypoponera nitidula	84	Strumigenys gundlachi	57	Solenopsis geminata	40	S. gundlachi	28	Megalomyrmex sp.2	43
Strumigenys elongata	66	Strumigenys sp. 6	57	Pheidole specularis	34	B. minutus	24	Carebara urichi	39

b)   Sierra de las Minas 90 species and morphospecies of ant total

Forest		Coffee		Cardamom		Fallow	
Wasmannia auropunctata	1270	Wasmannia auropunctata	2159	Wasmannia auropunctata	1006	Wasmannia auropunctata	402
Pheidole deceptrix	370	Carebara urichi	476	Octostruma balzani	398	Cyphomyrmex salvini	318
Pheidole browni	289	Octostruma balzani	331	Labidus coecus	274	Carebara intermedia	257
Brachymyrmex minutus	242	Carebara intermedia	323	Strumigenys gundlachi	266	Octostruma balzani	177
Strumigenys timicala	212	Strumigenys gundlachi	180	Carebara intermedia	242	Strumigenys gundlachi	152
Strumigenys gundlachi	191	Solenopsis geminata	132	Paratrechina longicornis	225	Brachymyrmex minutus	124
Adelomyrmex paratristani	189	Pheidole harrisonfordi	65	Carebara urichi	163	Strumigenys brevicornis	90
Cyphomyrmex rimosus	148	Brachymyrmex minutus	61	Pheidole harrisonfordi	162	Brachymyrmex sp. 2	85
Strumigenys brevicornis	148	Brachymyrmex sp. 2	53	Strumigenys margaritae	156	Pheidole beloceps	70
Octostruma balzani	135	Hypoponera nitidula	46	Pheidole beloceps	137	Pheidole browni	64

Table B.3. Most common Cicadellidae species in each land-use in Guatemala. Number of individuals sampled is given after each name

a)   Palajunoj - 68 species and morphospecies in total

Forest		Inga-coffee		Agroforest Coffee		Rubber		Macadamia	
Typhlocybella sp4	18	Agallinae sp1	161	Deltocephalinae sp4	65	Agallinae sp1	97	Agallinae sp1	185
Tylozygus geometricus	17	*Tylozygus geometricus*	35	Typhlocybella sp2	63	Typhlocybella sp4	22	Typhlocybella sp4	39
Typhlocybella sp5	10	Typhlocybella sp4	35	Agallinae sp1	48	*Tylozygus geometricus*	19	*Tylozygus geometricus*	22
Aphrodinae sp4	10	Typhlocybella sp5	18	*Tylozygus geometricus*	46	Agallinae sp2	12	Typhlocybella sp5	17
Typhlocybinae sp5	8	Polyamia* sp1	16	Typhlocybella sp4	44	Polyamia* sp1	11	Cicadellidae 32	14
Osbornellus* sp3	8	Deltocephalinae sp4	15	Typhlocybella sp5	27	*Macunolla ventralis*	8	*Macunolla intorta*	13

b)   Sierra de las Minas – 64 species and morphospecies total

Forest		Coffee		Cardomom		Fallow	
Agallinae sp2	7	*Tylozygus geometricus*	30	*Tylozygus geometricus*	26	Agallinae sp1	41
Aphrodinae sp4	5	Typhlocybella sp2	29	Typhlocybella sp2	23	Typhlocybella sp2	39
Typhlocybella sp2	5	Graphocephala* sp2	24	Agallinae sp1	18	Agallinae sp2	20
Graphocephala* sp2	3	Agallinae sp1	17	Agallinae sp2	9	Aphrodinae sp3	13
		Agallinae sp2	11	*Graphocephala aurolineata*	4	Forcipata sp1	8
		Stirellus bicolor	6	Graphocephala* sp2	4	*Tylozygus geometricus*	6

Appendix C Non-metric multidimensional scaling graphs comparing species composition across land-uses for each taxonomic group in each landscape.

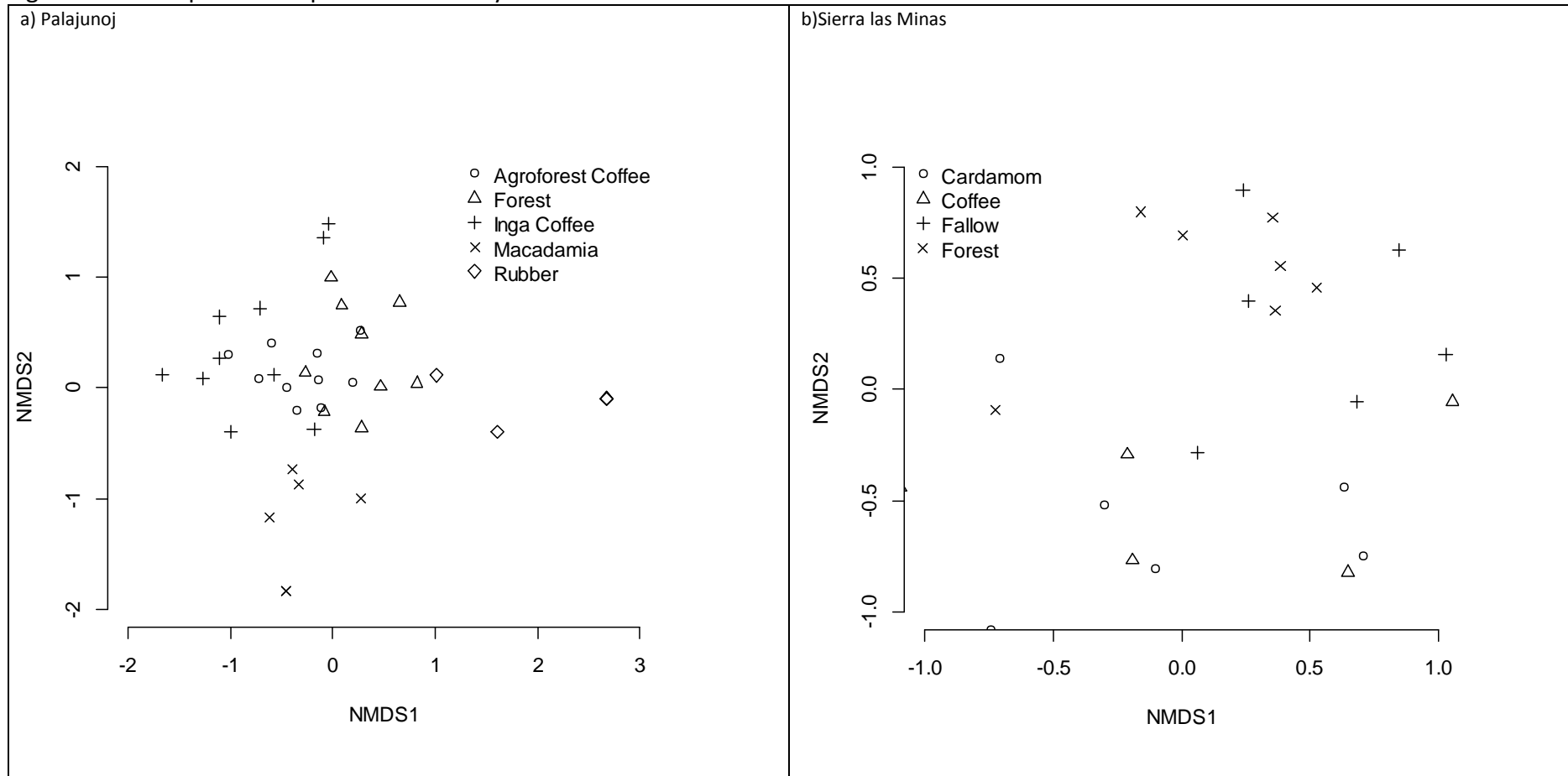Figure C.1 Tree species composition similarity between land-uses

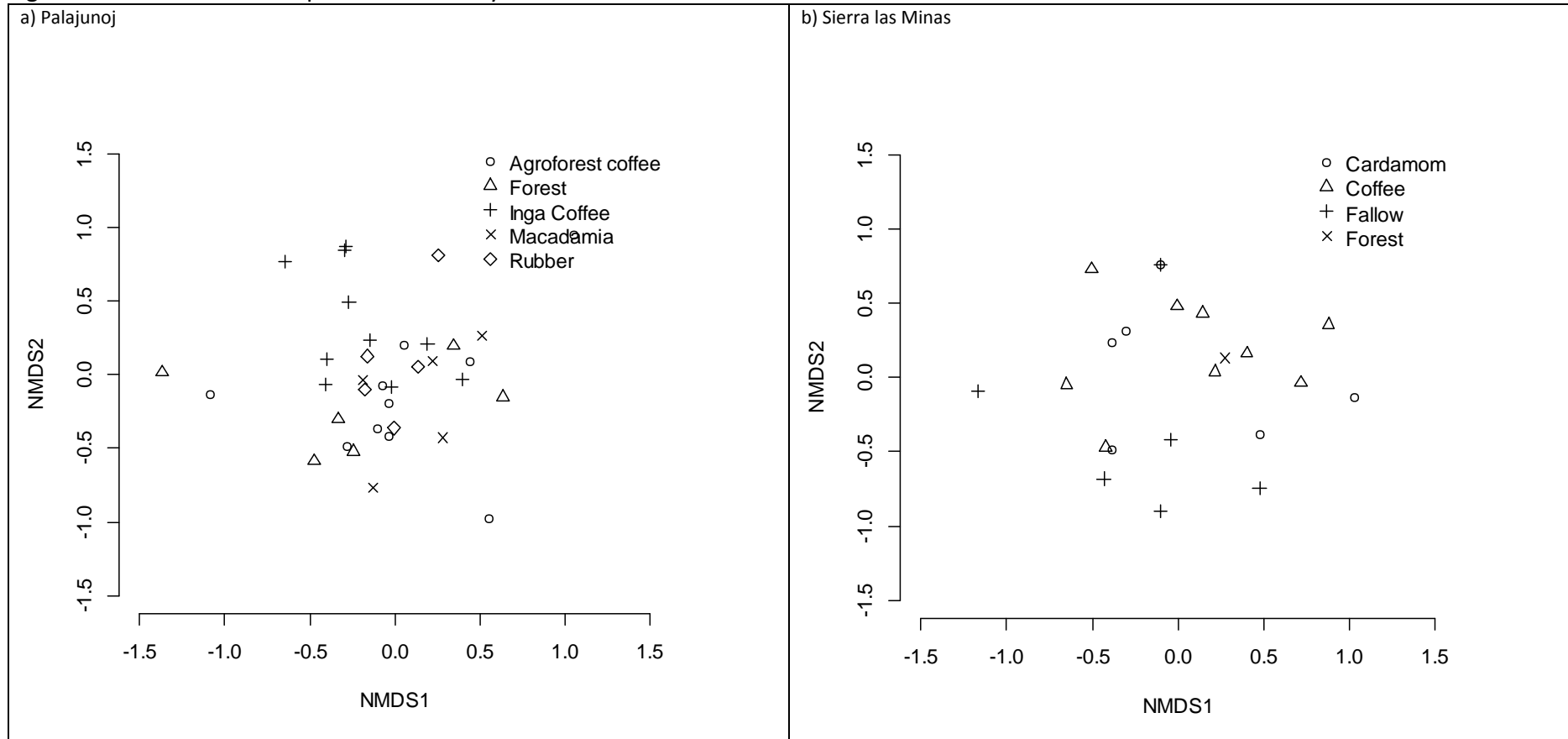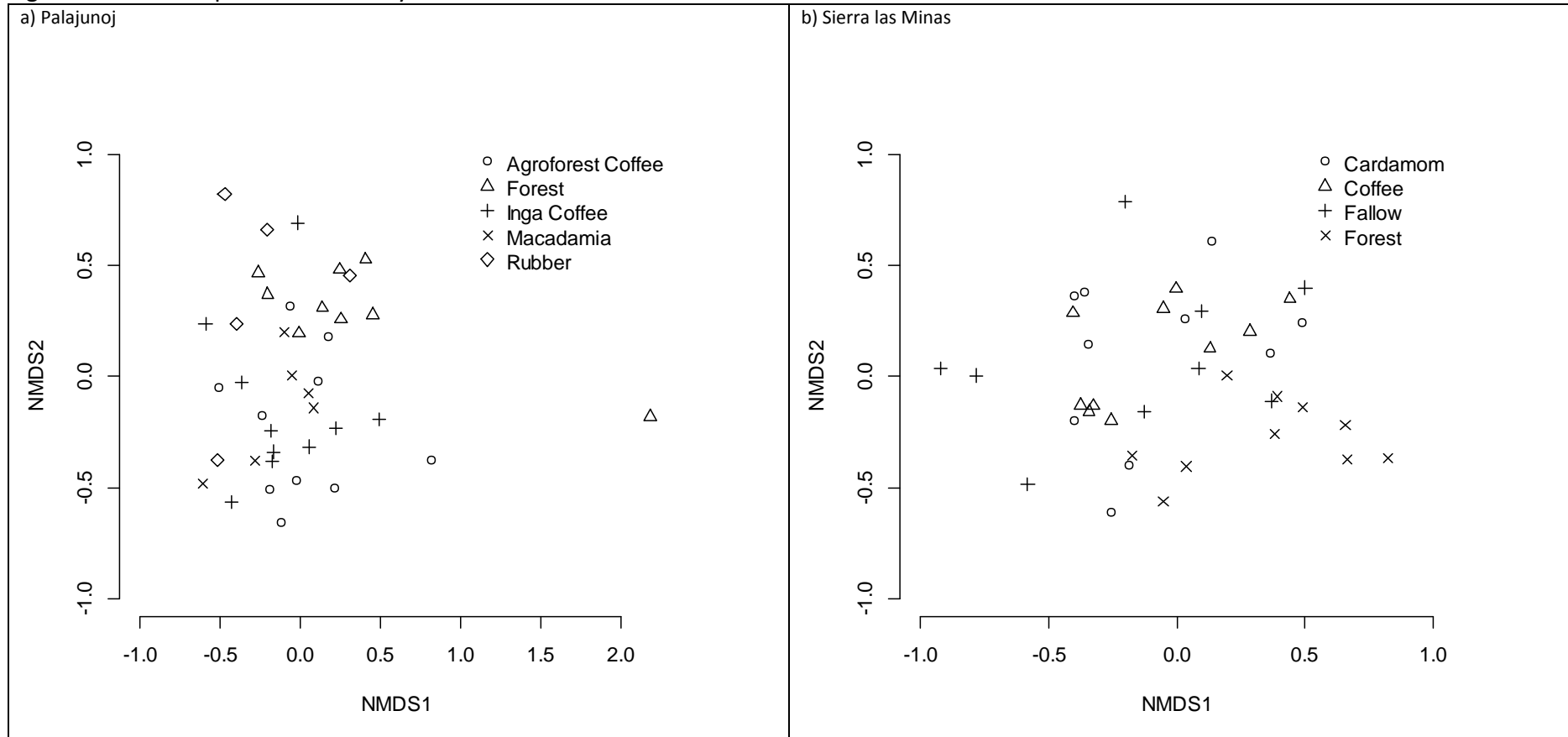Figure C.2 Cicadellidae composition similarity between land-uses

Figure C.3 Ant composition similarity between land-uses

Appendix D: Maps of land-use and connectivity in two study landscapes

Figure D1. Land-use map of a) Palajunoj (lowest altitude is at the bottom (South) of the map) and b) Sierra de las Minas (lowest altitude is at the top (North) of the map).
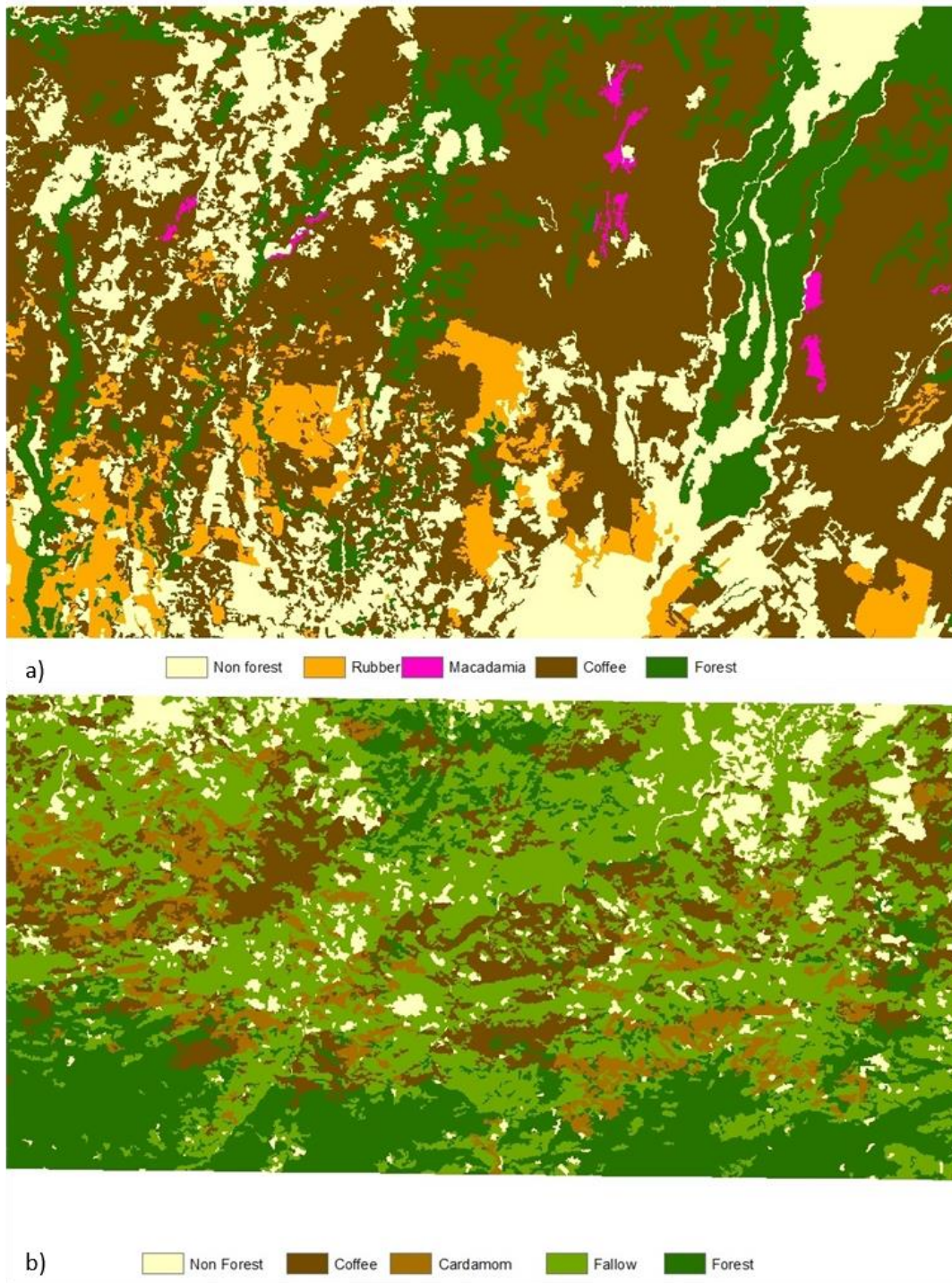
Figure D2. Forest biodiversity connectivity in Palajunoj under different land-use scenarios; 1 = forest, 2 = forest+coffee, 3=forest+coffee+macadamia, 4=forest+coffee+macadamia+rubber
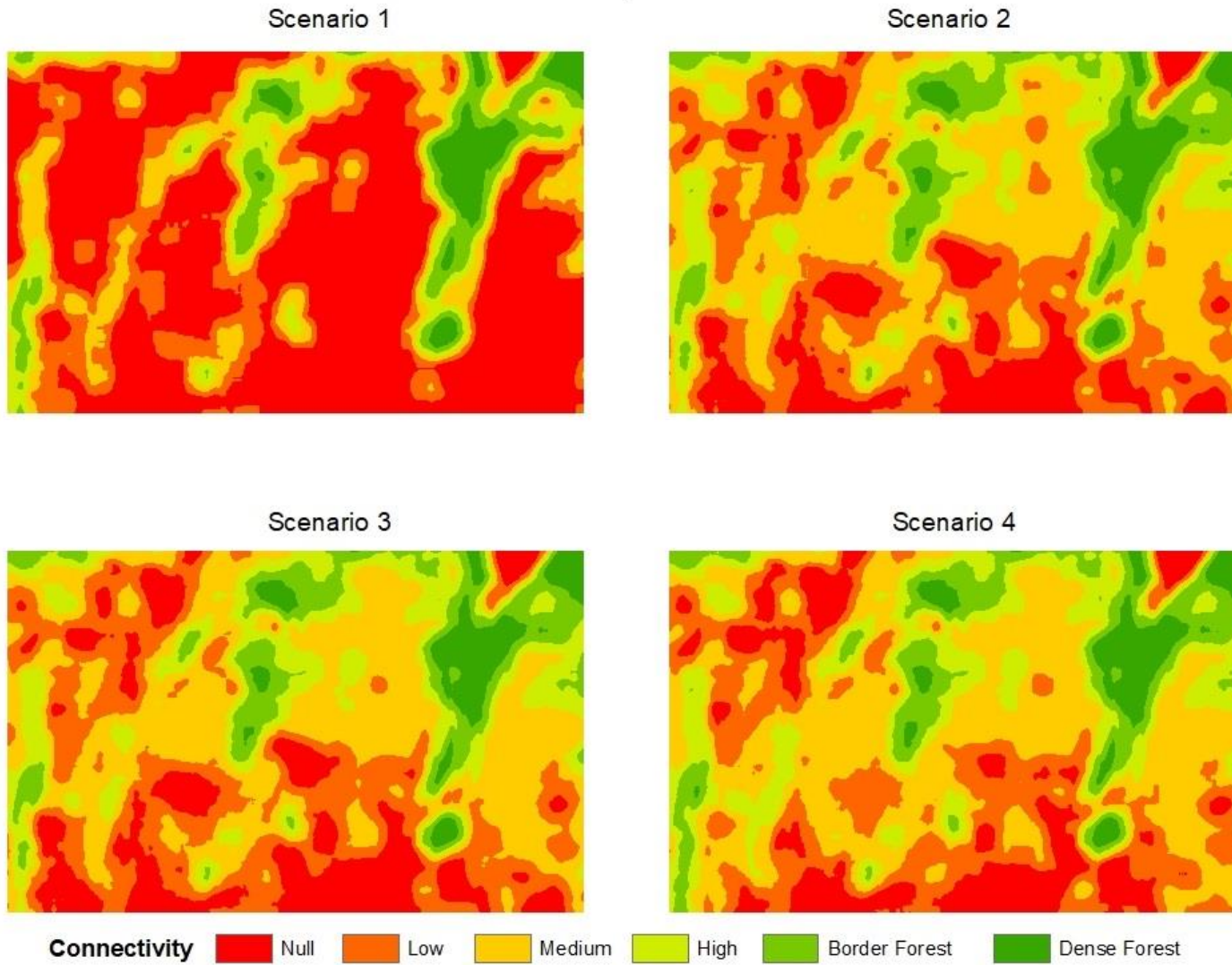
Figure D3. Forest biodiversity connectivity for Sierra de las Minas landscape under different scenarios; 1 = forest, 2 = forest+fallow, 3=forest+fallow+cardamom, 4=forest+fallow+cardamom+coffee.