

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.

33

### 34 **Keywords**

35 Coffee; connectivity; fallow; landscape; rubber; species richness.

36

37

## 38 1. Introduction

39 Faced with the current threats to biodiversity such as climate change, invasive species,  
40 deforestation, and disruption of migration paths by infrastructure and human settlements, protected  
41 areas are insufficient to preserve biodiversity (DeFries et al. 2005; Millennium Ecosystem Assessment  
42 2005). Therefore, agroecosystems need to play a complementary role to protected areas in the  
43 conservation of biodiversity (Vandermeer and Perfecto 2007; Harvey et al. 2008). The combination of  
44 crops with diverse tree assemblages in agroforestry systems have been found to maintain high levels  
45 of both flora and fauna (Tscharntke et al. 2011). Agroforestry has the potential to contribute to  
46 biodiversity conservation by creating habitat for species which are tolerant to some level of  
47 disturbance (Harvey and Villalobos, 2007). Agroforestry systems have therefore been proposed for  
48 use in buffer zones or biological corridors, as habitats for such species (Donald 2004; Mas and Dietsch  
49 2004).

50

51 Agroforestry systems sustain higher biodiversity than agricultural systems through having  
52 greater plant diversity (including native species), increased structural complexity, and enhanced  
53 habitat and landscape heterogeneity. Tree species richness has been found to have close correlation  
54 with the diversity of fruit and nectar-feeding birds and fruit-feeding butterflies (Schulze et al. 2004)  
55 and with the diversity of arthropod groups such as ants (Leal et al. 2012). There have been numerous  
56 studies on different taxonomic groups in coffee agroforestry (often called shaded coffee) including  
57 migratory birds (Bakermans et al. 2009), orchids (Solis-Montero et al. 2005), bats (Estrada et al. 2006),  
58 ants (Armbrecht et al. 2005), and amphibians (Santos-Barrera et al. 2011), showing the potential for  
59 this system to conserving these species. The nature of the shade in coffee (and similar crops like cocoa  
60 or cardamom) varies considerably from heavily managed single species shade to highly diverse tree  
61 species assemblages (Moguel and Toledo 1999). In a metanalysis of studies comparing the relative  
62 biodiversity of forest, and coffee and cocoa agroforestry and monocultures, Beenhouwer et al (2013)  
63 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. Hagggar 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, Hagggar 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 (Haggard 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<sup>2</sup>. 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<sup>2</sup>.

129

## 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<sup>2</sup> 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.

186

#### 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

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

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

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. Hagggar 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. Hagggar 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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420

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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		

530

531

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

Taxa / Land use	Total number of species in land-use	Number of species in paired forest plots*	Shared species %	Chao- Sorensen n	Estimated S.D.	Morisita- Horn
<u>Trees</u>						
Inga coffee	45	89	32.8	0.548	0.11	0.076
Agroforest						
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
<u>Ants</u>						
Inga coffee	53	55	70.4	0.997	0.022	0.610
Agroforest						
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
<u>Cicadellidae</u>						
Inga coffee	28	28	46.4	0.753	0.076	0.298
Agroforest						
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

534 \*The number of species in forest varies when compared with macadamia and rubber because the  
 535 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	Shared	Chao- Sorensen	Estimated S.D.	Morisita- Horn
	number of species in land-use	species in paired forest plots				
<u>Trees</u>						
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
<u>Ants</u>						
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
<u>Cicadellidae</u>						
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

539

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541

542

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	Contribution to final estimate of connectivity	Average connectivity index	Contribution to final estimate of connectivity	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%

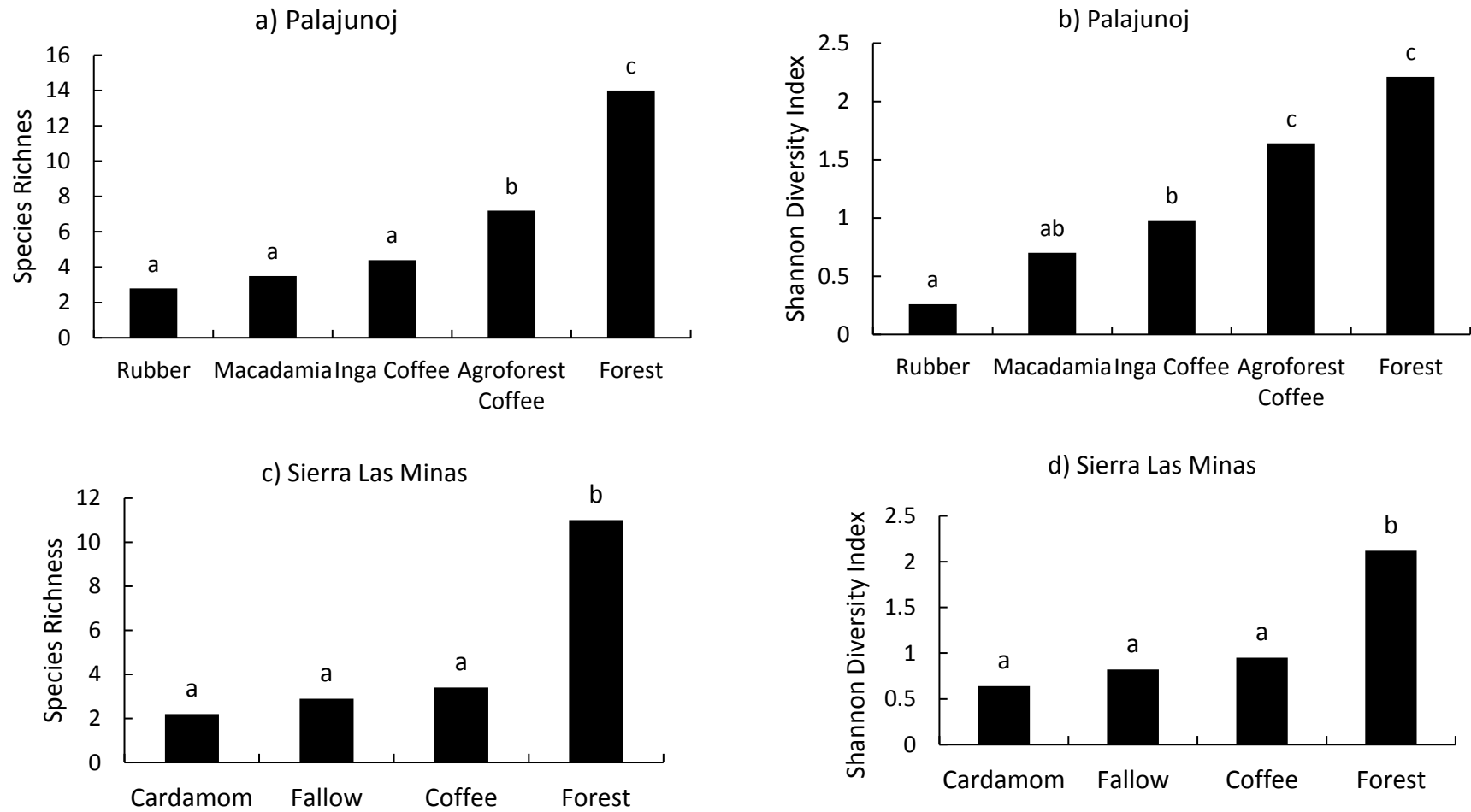
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547 Figure Legends

548

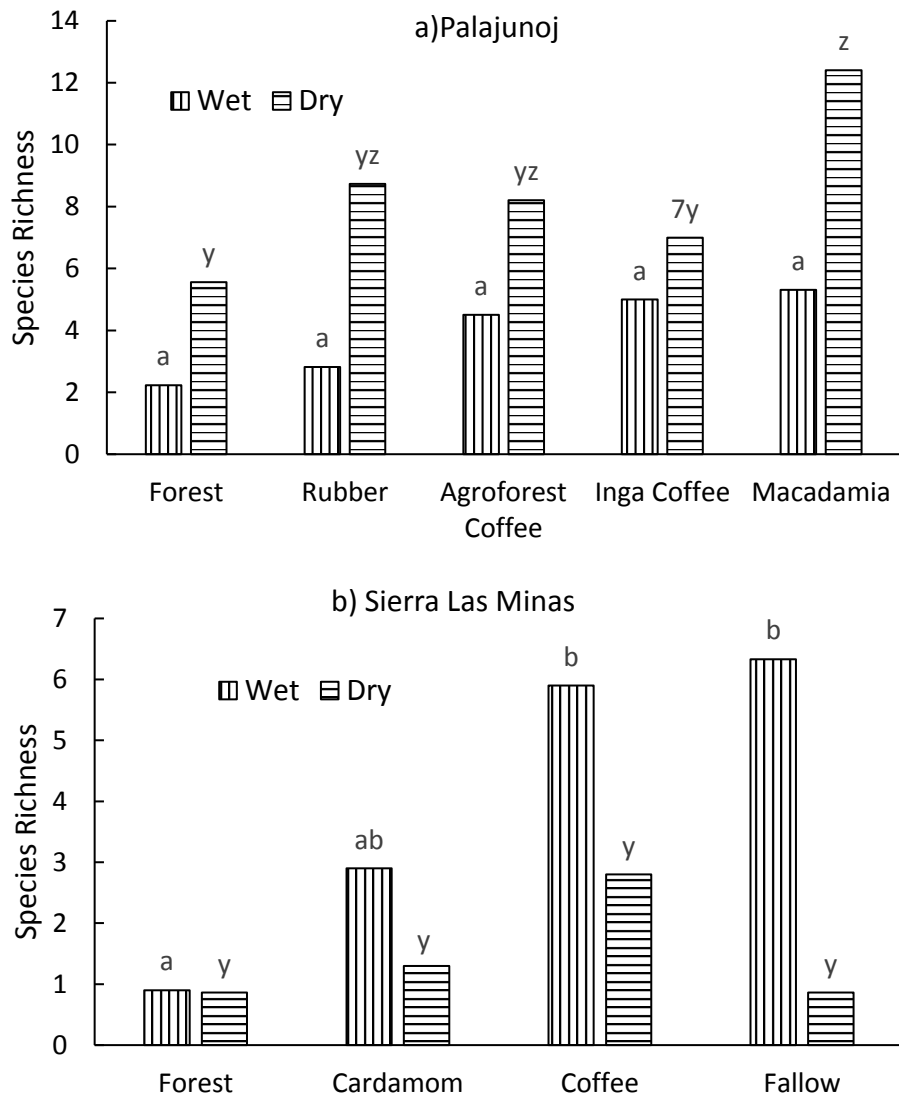
549 Fig. 1 Tree species richness (a. in Palajunoj and c. Sierra Las Minas) and Shannon Diversity Index (b. in Palajunoj and d. in Sierra Las Minas) under different  
 550 land-uses in two landscapes in Guatemala. Columns that do not share the same letter are significantly different ( $p < 0.05$ ).



551

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 ( $p < 0.05$ ).

555



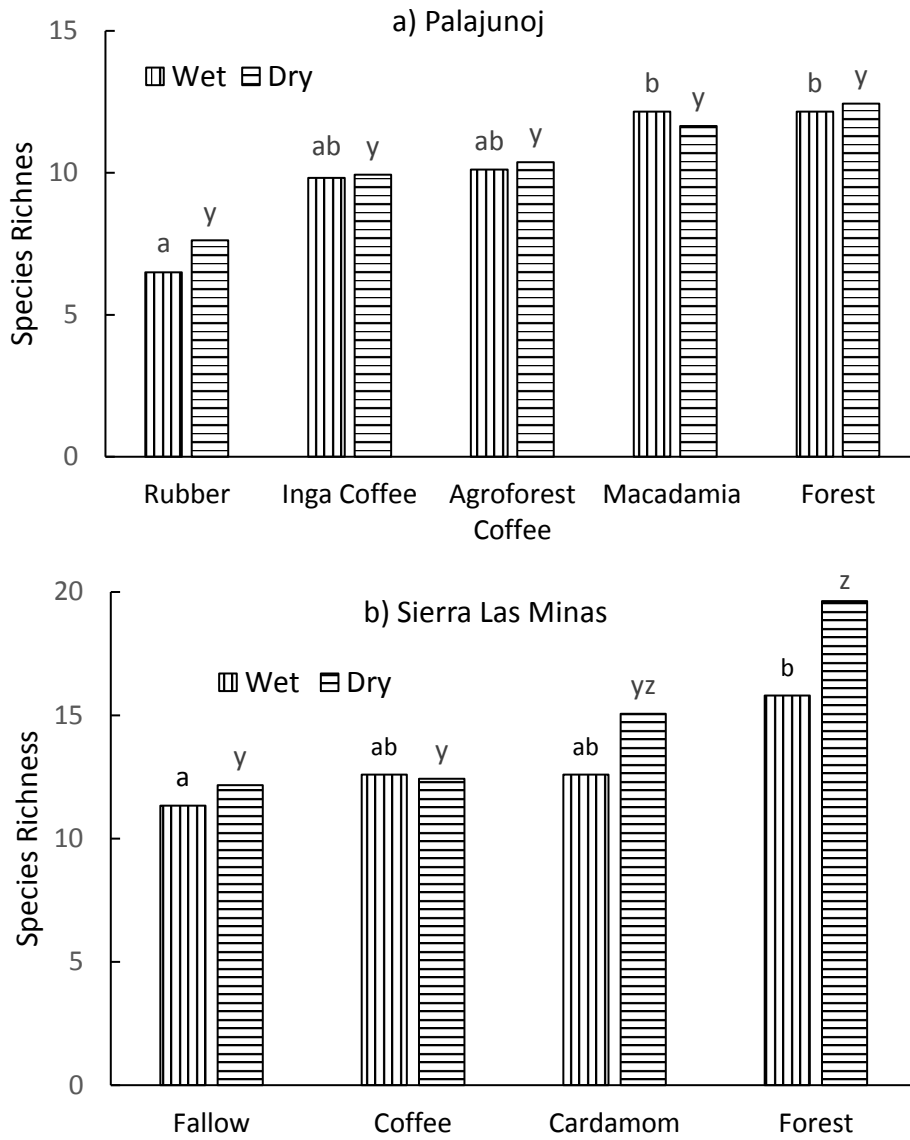
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558

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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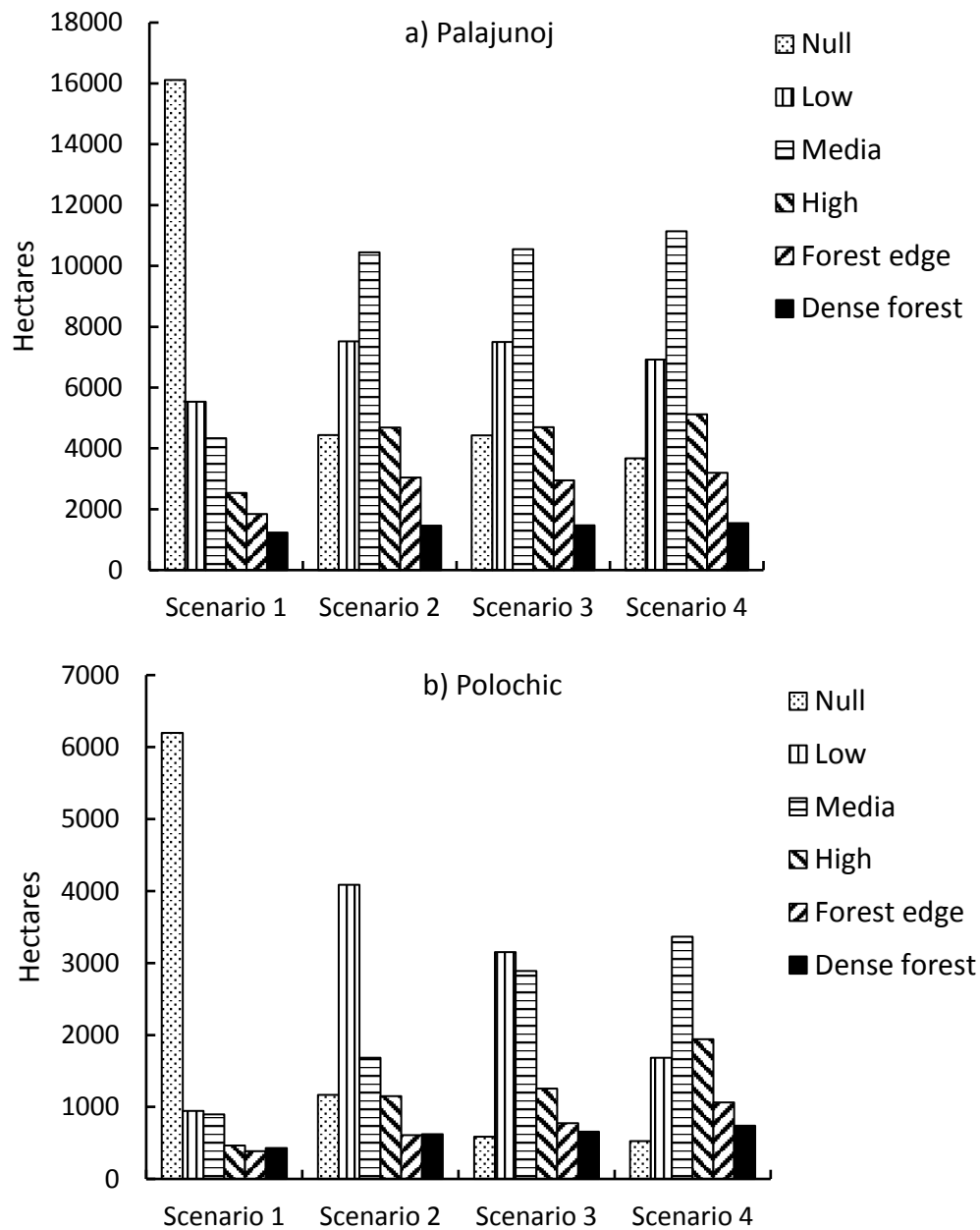
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566

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).

572



573

## 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
<b>Total</b>	<b>26,732</b>		<b>Total</b>	<b>11,590</b>	

\*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

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

### b) Sierra de las Minas – 86 tree species total

<b>Forest (225)</b>	<b>Coffee (65)</b>	<b>Cardamom (58)</b>	<b>Fallow (56)</b>
<i>Miconia</i> sp. (21)	<i>Inga spuria</i> (11)	<i>Saurauia villosa</i> (17)	<i>Miconia</i> sp. (23)
<i>Saurauia villosa</i> (17)	<i>Gliricidia sepium</i> (10)	<i>Aegiphila monstrosa</i> (14)	Ch'ut (6)
<i>Ficus</i> sp. (12)	<i>Calophyllum brasiliense</i> (5)	<i>Swietenia macrophylla</i> (7)	Joow (5)
<i>Hyeronima oblonga</i> (10)	<i>Aegiphila monstrosa</i> (5)	<i>Inga edulis</i> (4)	Ch'eer (4)
<i>Calophyllum brasiliense</i> (9)	<i>Saurauia villosa</i> (4)	<i>Hevea brasiliensis</i> (4)	<i>Cecropia peltata</i> (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	
<i>Pheidole harrisonfordi</i>	414	<i>W. auropunctata</i>	883	<i>P. harrisonfordi</i>	779	<i>Carebara urichi</i>	635	<i>P. harrisonfordi</i>	585
<i>Wasmannia auropunctata</i>	325	<i>Pheidole harrisonfordi</i>	558	<i>Wasmannia auropunctata</i>	131	<i>Pheidole harrisonfordi</i>	211	<i>Solenopsis geminata</i>	272
<i>Carebara urichi</i>	320	<i>Solenopsis geminata</i>	311	<i>Carebara urichi</i>	115	<i>Gnamptogenys strigata</i>	67	<i>Brachymyrmex</i> sp.2	215
<i>Octostruma balzani</i>	272	<i>Carebara urichi</i>	222	<i>Octostruma balzani</i>	115	<i>Octostruma balzani</i>	55	<i>Labidus coecus</i>	187
<i>Carebara intermedia</i>	270	<i>Acropyga exsanguis</i>	150	<i>Gnamptogenys strigata</i>	96	<i>Wasmannia auropunctata</i>	53	<i>Octostruma balzani</i>	88
<i>Strumigenys brevicornis</i>	121	<i>Brachymyrmex minutus</i>	142	<i>Hypoponera nitidula</i>	72	<i>Carebara intermedia</i>	52	<i>Brachymyrmex minutus</i>	77
<i>Strumigenys gundlachi</i>	116	<i>Octostruma balzani</i>	81	<i>Brachymyrmex minutus</i>	49	<i>Strumigenys elongata</i>	48	<i>Strumigenys gundlachi</i>	61
<i>Stenamamma nonotch</i>	98	<i>Strumigenys elongata</i>	57	<i>Carebara intermedia</i>	41	<i>Brachymyrmex</i> sp. 2	37	<i>Strumigenys</i> sp. 6	45
<i>Hypoconera nitidula</i>	84	<i>Strumigenys gundlachi</i>	57	<i>Solenopsis geminata</i>	40	<i>S. gundlachi</i>	28	<i>Megalomyrmex</i> sp.2	43
<i>Strumigenys elongata</i>	66	<i>Strumigenys</i> sp. 6	57	<i>Pheidole specularis</i>	34	<i>B. minutus</i>	24	<i>Carebara urichi</i>	39

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

Forest		Coffee		Cardamom		Fallow	
<i>Wasmannia auropunctata</i>	1270	<i>Wasmannia auropunctata</i>	2159	<i>Wasmannia auropunctata</i>	1006	<i>Wasmannia auropunctata</i>	402
<i>Pheidole deceptrix</i>	370	<i>Carebara urichi</i>	476	<i>Octostruma balzani</i>	398	<i>Cyphomyrmex salvini</i>	318
<i>Pheidole browni</i>	289	<i>Octostruma balzani</i>	331	<i>Labidus coecus</i>	274	<i>Carebara intermedia</i>	257
<i>Brachymyrmex minutus</i>	242	<i>Carebara intermedia</i>	323	<i>Strumigenys gundlachi</i>	266	<i>Octostruma balzani</i>	177
<i>Strumigenys timicala</i>	212	<i>Strumigenys gundlachi</i>	180	<i>Carebara intermedia</i>	242	<i>Strumigenys gundlachi</i>	152
<i>Strumigenys gundlachi</i>	191	<i>Solenopsis geminata</i>	132	<i>Paratrechina longicornis</i>	225	<i>Brachymyrmex minutus</i>	124
<i>Adelomyrmex paratristani</i>	189	<i>Pheidole harrisonfordi</i>	65	<i>Carebara urichi</i>	163	<i>Strumigenys brevicornis</i>	90
<i>Cyphomyrmex rimosus</i>	148	<i>Brachymyrmex minutus</i>	61	<i>Pheidole harrisonfordi</i>	162	<i>Brachymyrmex</i> sp. 2	85
<i>Strumigenys brevicornis</i>	148	<i>Brachymyrmex</i> sp. 2	53	<i>Strumigenys margaritae</i>	156	<i>Pheidole beloiceps</i>	70
<i>Octostruma balzani</i>	135	<i>Hypoconera nitidula</i>	46	<i>Pheidole beloiceps</i>	137	<i>Pheidole browni</i>	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
<i>Tylozygus geometricus</i>	17	<i>Tylozygus geometricus</i>	35	Typhlocybella sp2	63	Typhlocybella sp4	22	Typhlocybella sp4	39
Typhlocybella sp5	10	Typhlocybella sp4	35	Agallinae sp1	48	<i>Tylozygus geometricus</i>	19	<i>Tylozygus geometricus</i>	22
Aphrodinae sp4	10	Typhlocybella sp5	18	<i>Tylozygus geometricus</i>	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	<i>Macunolla ventralis</i>	8	<i>Macunolla intorta</i>	13

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

Forest		Coffee		Cardomom		Fallow	
Agallinae sp2	7	<i>Tylozygus geometricus</i>	30	<i>Tylozygus geometricus</i>	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
				<i>Graphocephala</i>			
		Agallinae sp2	11	<i>aurolineata</i>	4	Forcipata sp1	8
		Stirellus bicolor	6	Graphocephala* sp2	4	<i>Tylozygus geometricus</i>	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

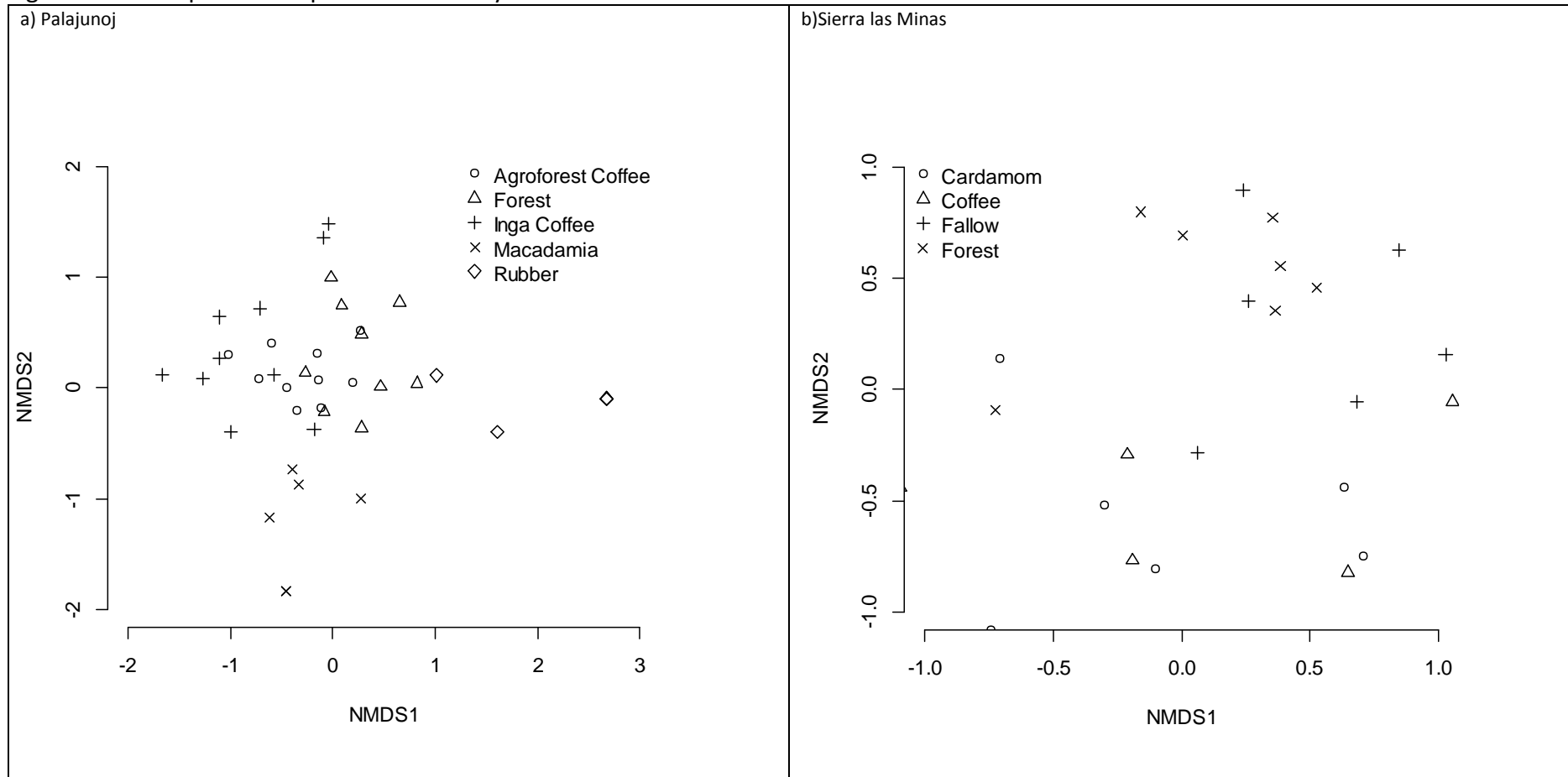


Figure C.2 Cicadellidae composition similarity between land-uses

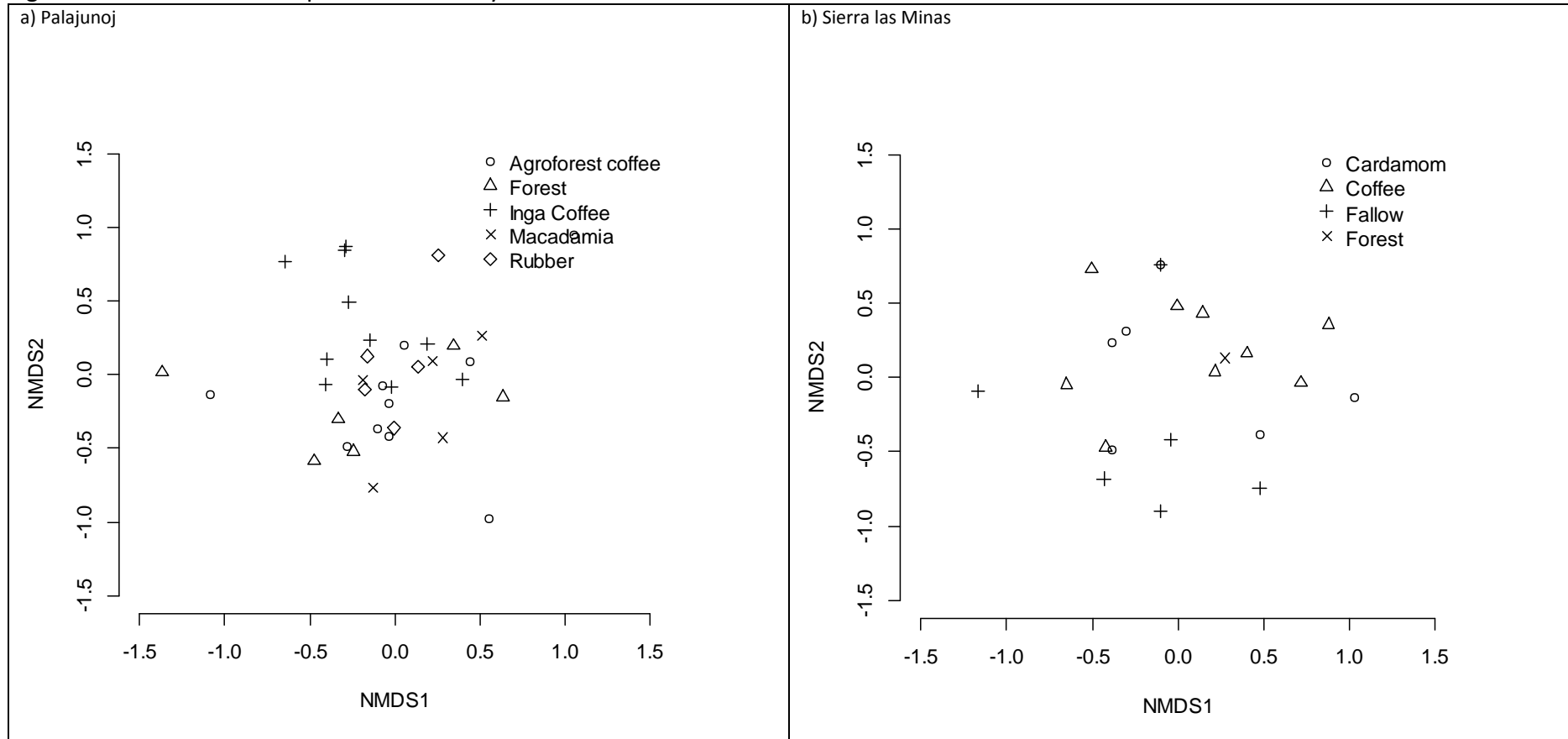
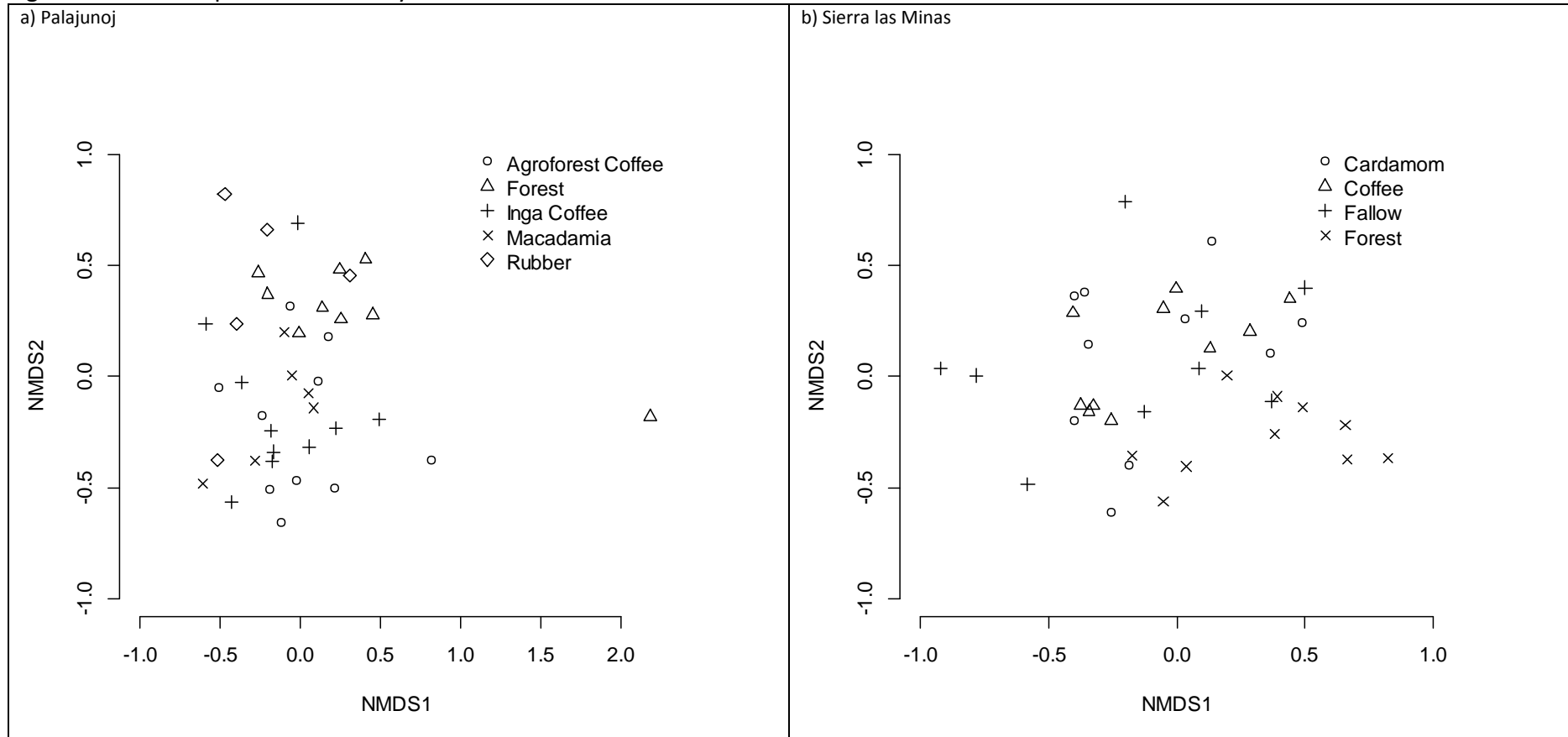


Figure C.3 Ant composition similarity between land-uses



## 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).

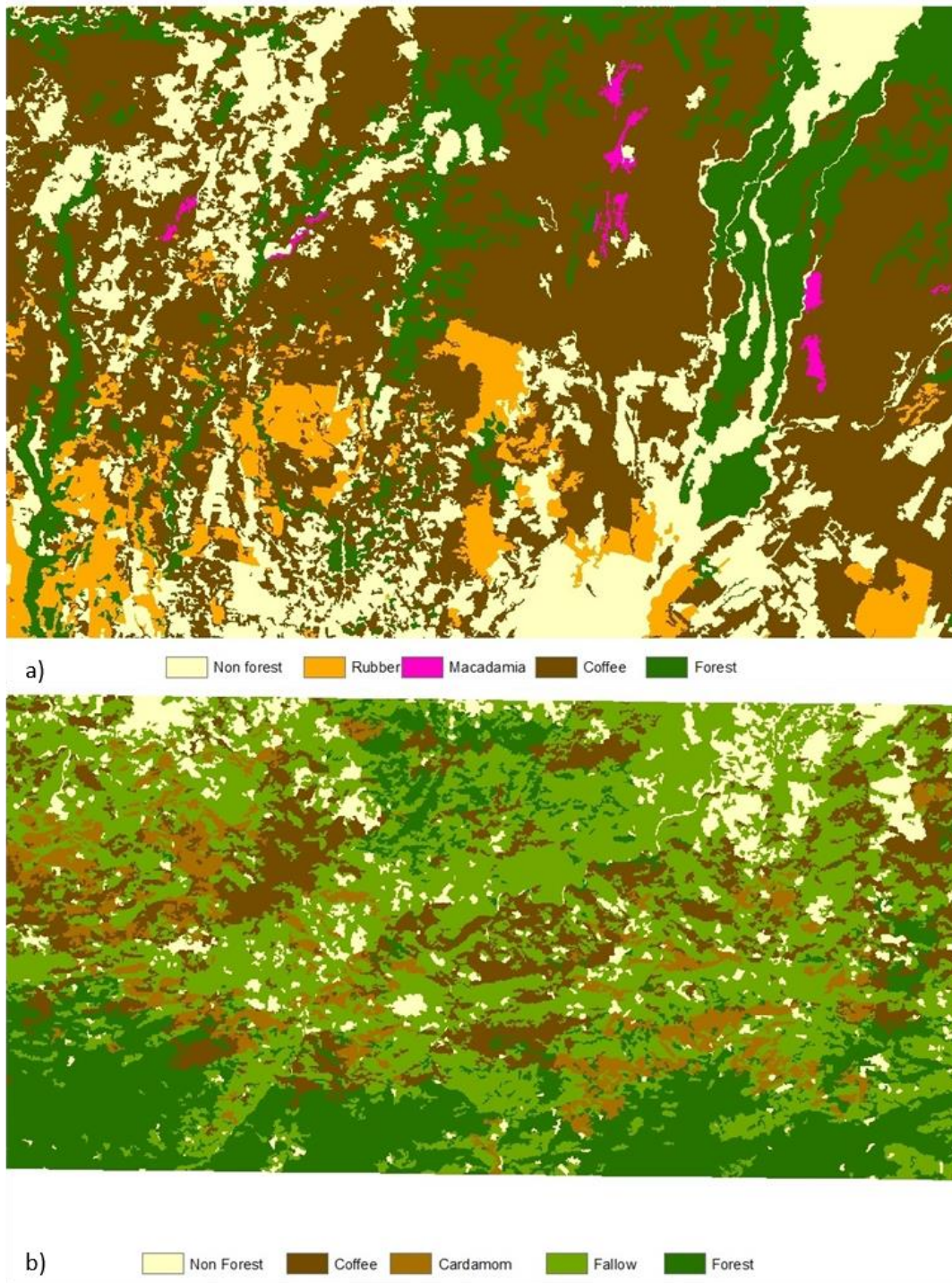


Figure D2. Forest biodiversity connectivity in Palajunoj under different land-use scenarios; 1 = forest, 2 = forest+coffee, 3=forest+coffee+macadamia, 4=forest+coffee+macadamia+rubber

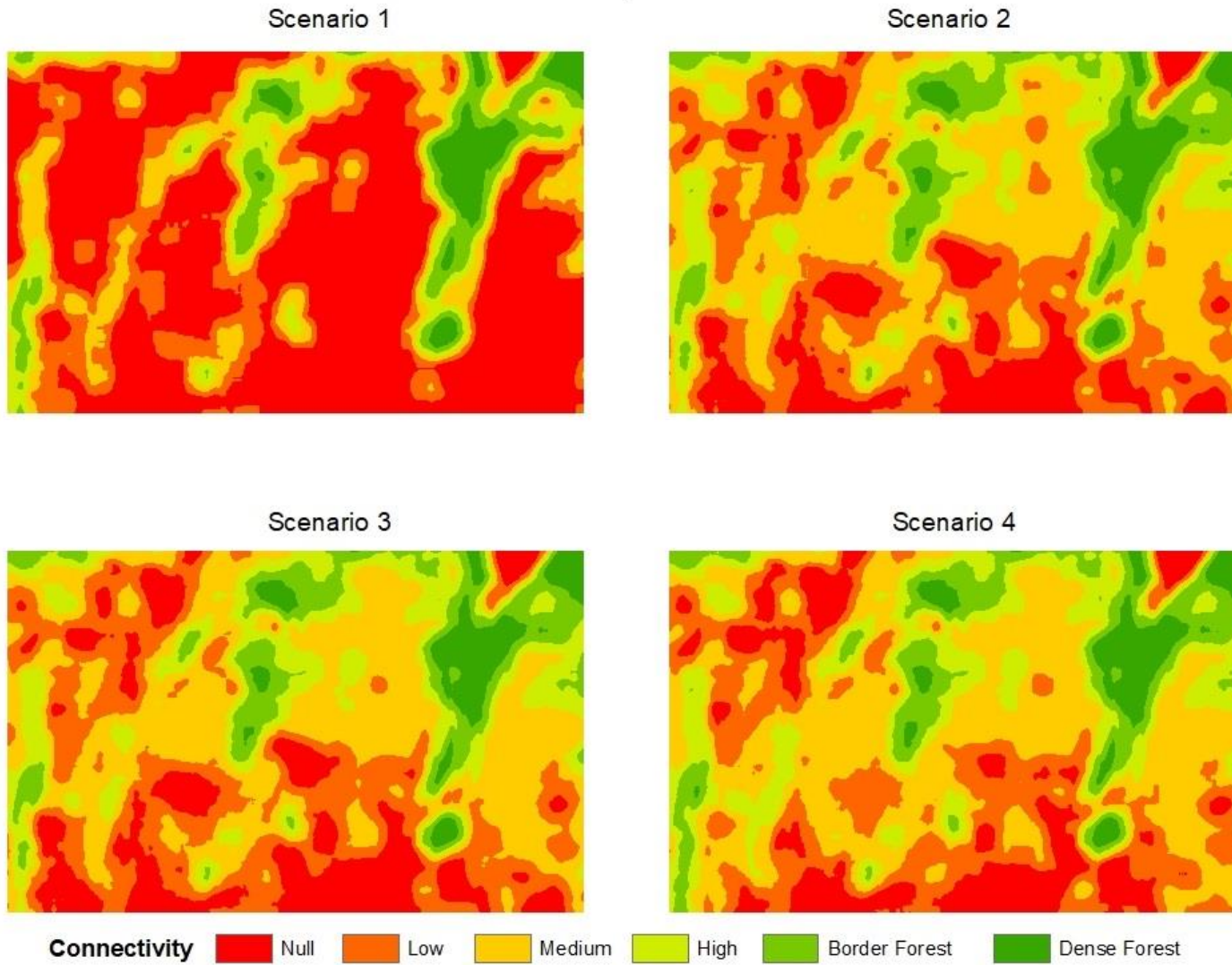




Figure D3. Forest biodiversity connectivity for Sierra de las Minas landscape under different scenarios; 1 = forest, 2 = forest+fallow, 3=forest+fallow+cardamom, 4=forest+fallow+cardamom+coffee.

