Effect of fragmentation on the Costa Rican dry forest avifauna

Gilbert Barrantes [1] , **Diego Ocampo** [1] , **José D. Ramírez-Fernández** [1] , **Eric J Fuchs** [Corresp. 1]

[1] Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica

Corresponding Author: Eric J Fuchs
Email address: e.j.fuchs@gmail.com

Deforestation and changes in land use have reduced the tropical dry forest to isolated forest patches in northwestern Costa Rica. We examined the effect of patch area and length of the dry season on nestedness of the entire avian community, forest fragment assemblages, and species occupancy across fragments for the entire native avifauna, and for a subset of forest dependent species. Species richness was independent of both fragment area and distance between fragments. Similarity in bird community composition between patches was related to habitat structure; fragments with similar forest structure have more similar avian assemblages. Size of forest patches influenced nestedness of the bird community and species occupancy, but not nestedness of assemblages across patches in northwestern Costa Rican avifauna. Forest dependent species (species that require large tracts of mature forest) and assemblages of these species nested along forest patches ranked by a gradient of seasonality, but only occupancy of species nested by area of patches. These results indicate that forest patches with a shorter dry season include a higher number of forest dependent species.

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4

5   Escuela de Biología, Universidad de Costa Rica, San Pedro, San José, Costa Rica. CP 2060

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7   **Abstract**: Deforestation and changes in land use have reduced the tropical dry forest to isolated forest

8   patches in northwestern Costa Rica. We examined the effect of patch area and length of the dry season on

9   nestedness of the entire avian community, forest fragment assemblages, and species occupancy across

10   fragments for the entire native avifauna, and for a subset of forest dependent species. Species richness

11   was independent of both fragment area and distance between fragments. Similarity in bird community

12   composition between patches was related to habitat structure; fragments with similar forest structure have

13   more similar avian assemblages. Size of forest patches influenced nestedness of the bird community and

14   species occupancy, but not nestedness of assemblages across patches in northwestern Costa Rican

15   avifauna. Forest dependent species (species that require large tracts of mature forest) and assemblages of

16   these species nested along forest patches ranked by a gradient of seasonality, but only occupancy of

17   species nested by area of patches. These results indicate that forest patches with a shorter dry season

18   include a higher number of forest dependent species.

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20   **Key words**: Forest size patches, habitat loss, bird composition, nested community analysis, community

21   similarity.

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37   INTRODUCTION

38   Deforestation and change in land use are the primary factors causing habitat deterioration and

39   forest fragmentation in tropical regions (Jaeger 2000, Lambin et al. 2003, Azevedo-Ramos *et al.* 2006,

40   Joyce 2006, Martínez et al. 2009). These changes on a natural landscape often reduce the capacity of

41   organisms to move across a matrix that consists of anthropogenic and semi-natural habitats (Renjifo 2001,

42   Graham and Blake 2001). Additionally, the negative effects of habitat loss and fragmentation are

43   intensified, as predation and competition tend to increase in forest patches (Andrén 1992, Fahrig 2003).

44   Thus, the direct and indirect negative effects of habitat loss and fragmentation could cause the extinction

45   of some species in the fragments, particularly of those species that rely on large tracts of mature forest for

46   reproduction (Stiles 1985).

47   Bird communities undergo notable changes in composition and abundance soon after large forests

48   are reduced into smaller patches (Bierregaard and Stouffer 1997, Oostra *et al.* 2008). In some cases

49   fragmentation could increase the abundance and richness of some bird species (Azevedo-Ramos *et al.*

50   2006) as birds aggregate in the remaining available forests patches. This increase in abundance and

51   richness is invariably followed by a steady reduction in diversity (Herkert 1994, Kruess and Tscharntke

52   1994, Lida and Nakashizuka 1995), because the available habitat is insufficient to sustain the large

53   number of species (Fahrig 2003, Pimm and Askins 1995). Additionally, invasion of non-forest bird-

54   species may increase competition for resources and increase parasite load, which in turn may further

55   reduce the reproductive success and viability of populations within fragments (Christiansen and Pitter

56   1997, Duncan 1997).

57   Reductions in genetic variability, demographic crashes and higher susceptibility to catastrophic

58   events have been hypothesized for resident bird populations in forest patches (Zuidema *et al.* 1996).

59   These effects may be prevented if fragments are interconnected or connected with larger continuous

60   forests (Haddad et al. 2003, Uezu et al. 2005). Unfortunately, given species-specific differences in

61   behavior, corridors are not suitable for all species (Rosenberg *et al.* 1997). Furthermore, newly

62   fragmented habitats are often difficult to re-connect with larger forest fragments or with other small

63   fragments; in most cases continuous habitats are impossible to recover. Hence, isolated forest patches

64   often become the only species reservoirs of previously widespread avifaunas.

65   Northwestern Costa Rican dry-forest has been reduced to 0.1% of its original extension and the

66   remaining forest consists of small patches surrounded by large cultivated areas (e.g., sugar cane, rice

67   field, cattle haciendas) (Janzen 1988, Quesada and Stoner 2004). Consequently, the original terrestrial

68   avifauna is now confined to these isolated, small forest patches; some of which are protected but with

69   little, if any, chance of reconnection. As a first approach to weigh the importance of these forest

70   fragments for the dry forest avifauna, we tested the effect of loss of natural habitat (Fahrig 2003, 2013) on

71   species composition in dry forests of northwestern Costa Rica at two different levels: the entire bird

72   community, and the assemblage of forest dependent species. We use nestedness analyses to test whether

73   fragmentation or the length of the dry season (i. e., seasonality gradient) produce a nested species pattern.

74   Testing if forest patches nest along a seasonal gradient provides information on the potential effect of

75   climate changes predicted for the region (Sheffield and Wood 2008). A nested pattern is expected when

76   species assemblages in species-poor sites are a subset of those assemblages present in species-rich sites

77   (patch nestedness), or when species occupying few sites are a subset of those species occupying a large

78   number of sites (species nestedness) (Novak *et al*. 2011). Hence nestedness may be the result of variation

79   in rates of colonization and extinction among sites (Lomolino 1996), or among species (Atmar and

80   Patterson 1993). We also test whether extinction (the likely cause of reduction of species across forest

81   fragments) is caused by either a reduction in patch size, an increase in the distance between forest

82   fragments as consequence of habitat deterioration, or if the nested pattern is associated with a climatic

83   gradient (i.e., seasonality) (Lomolino 1996, Wright *et al*. 1998).

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MATERIALS AND METHODS

87   **Data collection**

88   We gathered information on species composition from five forest fragments in northwestern

89   Costa Rica that varied in size and connectivity (Table 1, Fig.1): Parque Nacional Diriá (Dir), Reserva

90   Natural Absoluta Cabo Blanco (CB), Parque Nacional Palo Verde and the Reserva Biológica Lomas

91   Barbudal (PV), Parque Nacional Santa Rosa (SR), and Parque Nacional Rincón de la Vieja (RV). These

92   forest patches are surrounded by large agricultural fields and human communities (Joyce 2006) and the

93   distance between the nearest two forest patches included in this study is 58.9 km. There are some isolated

94   trees and small tracts of early successional vegetation in the matrix that surround forest patches, but they

95   are likely inadequate as corridors between patches. The fragmentation in the region has been the result of

96   a progressive loss of natural habitats due to transformation of these habitats into agricultural fields

97   (Boucher et al. 1983, Joyce 2006). We visited (GB, DO and JDRF) each site from 8 to 20 times to

98   compile a comprehensive bird list of each site during the last 15 years, starting in 2002. We sampled 3-4

99   days during each visit and searched for birds from 8 to 12 walking hours/day. In sites in which access is

100   difficult (e.g., RV) we extended the sampling period of each visit to 5-8 days, to reduce the number of

101   visits. Particularly during the breeding period of most dry forest birds (May through July) we focused our

102   efforts in detecting those elusive, rare species (e.g., some nightjars and cuckoos). We complemented our

103   survey data with information from Stiles (1983), checklist of SR and OTS (PV); Julio Sánchez and Luis

104   Sandoval provided us additional data for PV and RV respectively.

105   Climatically the northwestern region of Costa Rica is characterized by a long dry season from

106   December through May (Mata and Echeverría 2004) followed by a rainy season. However the local

107   conditions affect the length of the dry season across sites (Sánchez-Murillo et al. 2013), and this makes it

108   possible to order sites along a gradient of seasonality (Table 1). Precipitation patterns influence vegetation

109   in the region, which is dominated by deciduous vegetation with evergreen species along rivers, and

110   seasonal and permanent streams (Hartshorn 1983). We obtained the area of each patch, for statistical

111   analyses, from the Sistema Nacional de Areas de Conservación de Costa Rica (http://www.sinac.go.cr).

112   For PV we excluded the area covered by wetlands and included the area of the Reserva Biológica Lomas

113   Barbudal because it is connected with PV, and excluded the area on the Caribbean slope of RV because

114   this area is covered with rain forests rather than dry forests (Hartshorn 1983).

115   We excluded fresh water (e.g. Anatidae, Ardeidae) and marine birds (e.g. Fregatidae) from our

116   analyses because they are restricted to habitats that are not present in all sites. We also excluded

117   migratory birds. Occasional native species far from their normal geographic breeding distribution ranges

118   were also excluded. Thus, the dry-forest bird-community was composed of resident, breeding species

119   with terrestrial habits. Each bird species was classified into one of three forest dependency categories

120   following Stiles (1985) with modifications by Sandoval and Barrantes (2009): 1 = species that live and

121   reproduce in extensive mature forest; 2 = species that require habitats with 40-50% of forest cover; 3 =

122   species that inhabit open areas. Species in categories 1 and 2 are likely more affected by habitat loss than

123   those species included in category 3.

124

125   **Statistical analyses**

126   We used a Sørensen Similarity Index to evaluate similarity of bird species composition among

127   sites and assessed the relationship between species composition and geographic distances between sites

128   using a Mantel test. We also determined whether composition of resident species across dry forest patches

129   follows a nested distribution, or if each patch contains an independent subset of species, using the Vegan

130   package (version 1.17; http://cran.r-project.org) implemented in the R Statistical Language (version 3.00;

131   R Core Team 2015). A nested species distribution occurs when species richness in smaller fragments is a

132   subset of the richness of larger fragments. To test for nestedness in the avifauna of dry forest patches we

133   used presence/absence matrices in which rows and columns were patches and species respectively, and

134   then sorted rows (assemblages) and columns (species) by two criteria: along a gradient of patch sizes, and

135   along a gradient of rainfall seasonality. On these matrices we calculated the NODF metric (Almeida-Neto

136   *et al*. 2008, Ulrich *et al*. 2009, Moreira and Maltchik 2012) and used 999 permutations with the

137 'quasiswap' algorithm to estimate the model probability (Miklós and Podani 2004) by determining if the

138 estimated nestedness differed from a random (non-nested) distribution. 'Quasiswap' retains both rows

139 (sites) and columns (species) frequencies and does not increase Type I or Type II errors (Gainsbury and

140 Colli 2003). We used the NODF metric because it independently estimates nestedness of species

141 assemblages among sites (NODF rows), and nestedness for occupancy or presence among species (NODF

142 columns), and for the entire matrix that we refer to as community (Almeida-Neto *et al.* 2008). NODF, for

143 instance, calculates the nestedness of sites by comparing the occurrence of each species in each site (i.e.

144 fill or empty cells) with the marginal values corresponding to all sites, and then ranking the sites by a

145 previous determined gradient (e.g., area of fragments) (Almeida-Neto *et al.*, 2008). NODF is reported in

146 values ranging from 0 (not nested) to 100 (maximum nestedness). These models do not incorporate the

147 probability of detection of each species, but require that all (or nearly so) species from each fragment are

148 included.

149   We also inferred whether nestedness was either caused by differential extinction due to a

150 reduction in patch size or by rainfall seasonality (Cutler 1991, Lomolino 1996, Patterson 1990, Patterson

151 and Atmar 1986) conducting the statistical analyses described by Lomolino (1996): %PN = 100 x (R-

152 D)/R, where %PN = % of perfect nestedness, R = mean number of departures from random simulations,

153 and D = number of species that depart from perfect nestedness. To estimate the probability associated

154 with the D statistic, we took the ratio of species that depart from perfect nestedness, between the original

155 matrix and those obtained from 999 randomly generated matrices (scripts for running these analyses are

156 included as supplemental material). Lomolino's statistics were calculated for presence/absence species

157 matrix in which sites were first ordered by decreasing area and then along a gradient of seasonality (Fig.

158 1). Analyses were conducted for all the species and for forest dependent species (categories 1 and 2 of

159 forest dependence). With these matrices we tested if nestedness is caused by differential extinction due to

160 area reduction or rainfall seasonality.

161

162   RESULTS

163   We registered a total of 187 resident species in all study sites (Table S1). PV had the most

164 resident species while CB and Dir had the fewest, but the number of species did not differ significantly

165 across sites ($x^2 = 5.51$, df = 4, p = 0.239; Table 1). RV was least similar in species composition with

166 all other sites, and CB and Dir were most similar (Table 2). Species richness was independent of

167 both geographic distance (Mantel test = 0.42, p = 0.185; Table 2) and fragment area (r = 0.41, p =

168 0.494).

169   Patch size and rainfall were not correlated (Spearman = 0.70, p = 0.180), but both factors affected

170 similarly the nested pattern at three different levels: bird community (entire matrix), bird assemblages,

171 and species occurrence among dry forest patches. The community was significantly nested (based on

172 overlap and decreasing fill statistics - NODF) by size of dry forest patches (NODF = 31.6, p = 0.001).

173 Furthermore, species occupancy was nested among patches (NODF columns = 31.6, p = 0.001), but bird

174 assemblages were not nested by size of patches (NODF rows = 65.6, p = 0.099), though this probability

175 may imply nestedness, with the possibility of an outlier. The entire community also nested within forests

176 ranked by length of dry season (NODF = 31.6, p = 0.001). The bird assemblages showed a weak tendency

177 to be nested in patches ordered along this gradient of rainfall seasonality (NODF rows = 32.0, $0.05 < p < $

178 0.1) and species occupancy was strongly nested along such gradient (NODF columns = 31.6, p = 0.001).

179 The similarity of these results indicate that both factors affected the nestedness of species in dry forest

180 patches, but the small sample size (N = five patches) preclude us to test the interaction of both factors on

181 species nestedness.

182   The subset of forest dependent species (categories 1 and 2) was nested when considering area

183 (NODF = 24.17, p = 0.001) or seasonality (NODF = 24.15, p = 0.001) of dry forest fragments. Bird

184 assemblages of forest dependent species nested among forest fragments ranked along a seasonality

185 gradient (NODF rows = 42.15, p = 0.005), but not by area of fragments (NODF rows = 57.68, p = 0.397).

186 The species occupancy nested along both gradients: seasonality (NODF columns = 24.13, p = 0.001) and

187 area (NODF columns = 24.13, p = 0.001). According to Lomolino's test, differential extinction for the

188 entire community was not due to habitat loss (D = 121, R = 127.9, p = 0.386, %PN = 6.9), distance

189 between fragments (D = 120, R = 128.9, p = 0.336, %PN = 6.9), nor rainfall seasonality (D = 118, R =

190 128.7, p = 0.276, %PN = 8.3). Results are similar for forest dependent species (Table S2).

191   In general the proportion of species included in the three categories of forest dependency was

192 similar for all sites (x^2 = 7.7, df = 8, p = 0.468; Table 3). The number of forest dependent species

193 (category 1) did not differ across sites (x^2 = 5.1, df = 4, p = 0.167; Table 3). From this category 18 species

194 were detected in only one site and 72% of them were exclusively detected in RV (Table 3). Similarly, for

195 species in the category 2 we detected 58% only in RV. From the category 3 only four species were

196 detected in only one site.

197

198   DISCUSSION

199   Area did not explain the number of species found in these forest patches. This suggests that other

200 factors, such as environmental heterogeneity may also influence the number and/or composition of

201 species in fragments. For instance, patches with complex topography (e.g., altitudinal gradient,

202 mountains) often have higher species richness, or at least a different subset of species when compared

203 with patches with relatively homogeneous topographies (Primack 1998, Fernández-Juricic 2000, Mayr
204 and Diamond 2001). The characteristics of the matrix surrounding fragments, connectivity between
205 fragments, edge effect, and human interventions may also influence species richness within fragments
206 (Bierregaard and Stouffer 1997, Whitmore 1997).

207   In this study nestedness of the dry forest avifauna and forest dependent species is influenced by a
208 gradient of seasonality (length of dry season) and by fragment area. Sites with a shorter dry season
209 maintain a larger number of dry forest and forest dependent species. From a conservation perspective,
210 forest dependent species are likely more susceptible to global climatic changes, particularly to the
211 changes expected to occur as a consequence of the increasing frequency of ENSO events (Cai *et al.* 2014)
212 and the predicted intensification in the severity of droughts in the region (Sheffield and Wood 2008). Dry
213 forest dependent species require large mature forest tracts to maintain reproductive populations (Stiles
214 1985). However, both factors, ENSO events and severe droughts, result in longer and more severe dry
215 seasons which consequently increase the frequency of wild fires (Janzen 1986), affecting the
216 physiognomy of the dry forest, changing its composition and structure (Barlow and Peres 2004), and thus
217 affecting the avifauna associated to mature forest tracts.

218   Habitat loss did not apparently cause differential extinction (based on Lomolinos' test) of species
219 among forest patches. This lack of causality may be attributed to the effect of recent forest fragmentation
220 (1960-1980) on bird communities. The effect of isolation will only become evident as fragmentation
221 persists for longer periods of time (Barrantes *et al.* 2011). Furthermore, other factors may counteract the
222 signature of habitat loss (or distance between fragments) on nestedness. For instance, the high resilience
223 apparently inherent to dry forest birds (Barrantes and Sánchez 2004). Many dry forest birds are
224 presumably capable of maintaining small reproductive populations in suboptimal habitats (e.g., small
225 patches of secondary vegetation, pastures, Barrantes and Sánchez 2004). Other species (e.g., *Callocitta*
226 *formosa* and *Campylorhynchus rufinucha*) are capable of moving between distant forest fragments along
227 linear vegetation corridors or flying between isolated trees or bushes (Harvey *et al.* 2005). Thus, habitat
228 use and behavioral features of some dry forest bird species reduce the probability of detecting the
229 proximal causes of nestedness (e.g., habitat reduction and geographical isolation).

230   Species composition across sites may be related to vegetation features than to area of fragments
231 or geographic isolation. The area of the patches included in this study does not predict the number of
232 species present in each fragment. For instance, Santa Rosa nearly triples the area of PV, but they both
233 have similar species richness. Likewise, CB has only one fifth the area of Dir, but the number of species
234 is similar in both sites. SR and Palo Verde are primarily deciduous forest and small tracts of evergreen
235 vegetation (Hartshorn 1983) and both sites have a similar species composition. Dir and CB share also a
236 high percentage of species and both have more humid conditions than SR and PV and larger tracts of

237 evergreen forest, as a result of a shorter dry season (Janzen 1986, Sánchez-Murillo et al. 2013). On the

238 contrary, RV shares fewer species with other dry forest patches, and populations of many of these species

239 are well isolated by topographic barriers from other populations (Barrantes 2009, Barrantes et al. 2011).

240 The topography of RV is more complex and includes an altitudinal gradient covered by forests with

241 different structure (Janzen 1986). The differences in species composition across sites highlight two

242 important aspects: first that species composition should be analyzed at a finer scale taking forest structure

243 and composition into account; and second, that to preserve the rich dry forest avifauna it is necessary to

244 preserve ecosystem diversity, e.g., through habitat restoration and fragments connection.

245   Results in Table 3 indicate that between 5.3 to 11.8 % of all native species in dry forest patches

246 require large areas of mature forests and more than 40% of the species in each forest patch require at least

247 50% of forest cover for feeding and reproduction (Stiles 1985). Hence, forest patches in northwestern

248 Costa Rica support a large number of species that require large tracts of mature tropical dry forests in the

249 most threaten forest ecosystem in Mesoamerica (Janzen 1988). These patches are then an important

250 reservoir for the rich dry forest Mesoamerican avifauna (Stotz *et al*. 1996), including four endemic

251 species to the Pacific slope of Middle America dry forest region (Lesser Ground Cuckoo, Pacific Screech

252 Owl, Long Tailed Manakin, White Throated Magpie-Jay), but habitat destruction, the removal of isolated

253 trees and forest patches reduces connectivity and may drastically reduce the viability of populations in

254 remnant forest fragments. In these isolated small patches genetic variability may decrease rapidly (Evans

255 and Sheldon 2008, but see Fuchs and Hamrick 2010) and the recurrent catastrophic events caused

256 primarily by intentional fires (Quesada and Stoner 2004) seriously threaten the long-term maintenance of

257 bird populations.

258   In conclusion, forest patches in northwestern Costa Rica are reservoirs of a large portion of bird

259 species of the Pacific slope of Central American dry forests. However, species composition varies widely

260 across fragments possibly as a consequence of differences in vegetation, climatic and topographic

261 conditions. In northwestern Costa Rica, the reduction of the original dry forest into small, isolated patches

262 resulted in a nested pattern of both bird assemblages and species. The lack of connectivity between these

263 fragments and the recurrent intentional fires in the region, and the predicted global climatic changes

264 threaten the long-term population-viability of many bird species. Nestedness analyses proved to be an

265 important tool to evaluate the consequences of habitat loss of natural environments. Most important, this

266 method can be used periodically to evaluate the effect of changes in climate and land use on the avifuna

267 (or other animals) in forest patches.

268

269   ACKNOWLEDGMENTS

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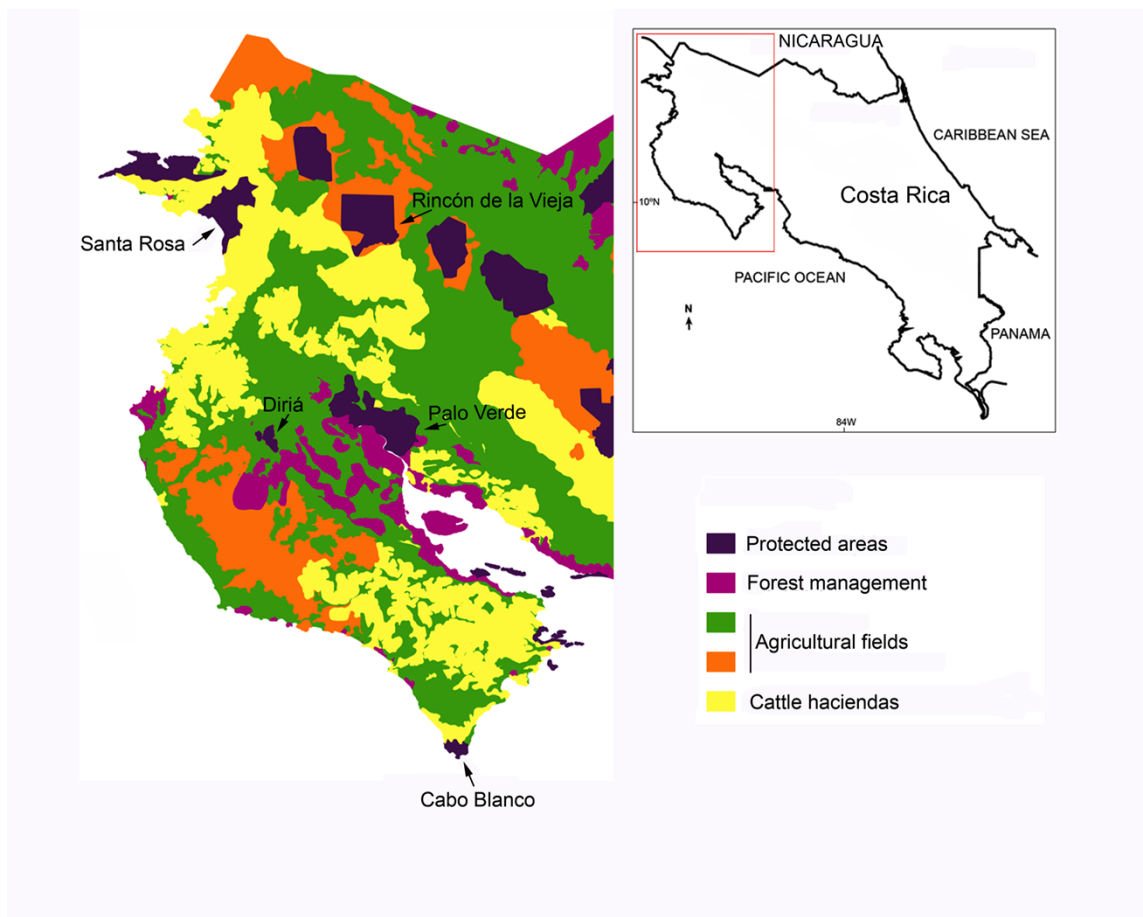409   Wright, D. H., B. D. Patterson, G. M. Mikkelson, A. Cutler and W. Atmar. 1998. A comparative analysis
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415 Fig.1. Dry forest fragments and areas with different use in northwestern Costa Rica. The inset shows the
416 map of Costa Rica.
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421   Table 1. Area, location and number of native species recorded in five dry forest fragments in northwestern
422   Costa Rica. Dry season includes the length of dry season in months and is based on meteorological
423   stations located in the same or nearby sites.

424

Locality	Dry season	Area (ha)	Location	No. of species
Santa Rosa	6-6.5	37117	10º50'N, 85º37'W	123
Palo Verde	5-5.5	11970	10º20'N, 85º20'W	135
Rincón de la Vieja	2-3	8411	10º49'N, 85º21'W	127
Diriá	4.5-5	5426	10º10'N, 85º35'W	109
Cabo Blanco	3-4	1172	09º33`N, 85º06'W	104

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428   Table 2. Sørensen similarity index and the number of species shared between sites in parentheses (below

429   the diagonal) and distance (km) (above the diagonal) between five forest patches in northwestern Costa

430   Rica. Higher values of the Sørensen similarity index indicate higher similarity in species composition

431   between sites.

432

		Distance				
		S. Rosa	P. Verde	Diria	C. Blanco	R. Vieja
Similarity	S. Rosa		77.9	72.6	71.5	63.6
	P. Verde	0.80 (116)		68.9	69.4	58.9
	Diria	0.82 (92)	0.71 (97)		70.6	61.3
	C. Blanco	0.81 (88)	0.67 (94)	0.85 (86)		64.6
	R. Vieja	0.73 (88)	0.62 (90)	0.70 (80)	0.76 (84)	

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436 Table 3. Species included in each category of forest dependence. The first row includes the total number

437 of species in each category and the number of species detected in a single sampling site. The other rows

438 include the number of species of that particular category detected in each site and the number of species

439 detected only in that particular site. The percentage of restricted species of each category per site is shown

440 in parenthesis.

441

Site	Category 1		Category 2		Category 3	
	No. species	Restricted	No. species	Restricted	No. species	Restricted
Total	33	18	101	26	53	4
Santa Rosa	10	0 (0)	71	1 (4)	42	0 (0)
Palo Verde	14	2 (11)	74	4 (15)	47	1 (25)
Diriá	14	3 (17)	58	2 (8)	37	2 (50)
C. Blanco	10	0 (0)	61	4 (15)	33	0 (0)
R. Vieja	22	13 (72)	70	15 (58)	35	1 (25

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