

Effect of fragmentation on the Costa Rican dry forest avifauna

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Abstract: 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~~ Thus, forest patches with a shorter dry season include a higher number of more forest dependent species.

Key words: Forest size patches, habitat loss, bird composition, nested community analysis, community similarity.

INTRODUCTION

Deforestation and change in land use are the primary factors causing habitat deterioration and forest fragmentation in tropical regions (Jaeger 2000, Lambin et al. 2003, Azevedo-Ramos et al. 2006, Joyce 2006, [Martínez](#) et al. 2009). These changes on a natural landscape often reduce the capacity of organisms to move across a matrix that consists of anthropogenic and semi-natural habitats (Renjifo 2001, Graham and Blake 2001). Additionally, the negative effects of habitat loss and fragmentation are intensified, as predation and competition tend to increase in forest patches (Andrén 1992, Fahrig 2003). Thus, the direct and indirect negative effects of habitat loss and fragmentation could cause the extinction of some species in the fragments, particularly of those species that rely on large tracts of mature forest for reproduction (Stiles 1985).

Bird communities undergo notable changes in composition and abundance soon after large forests are reduced into smaller patches (Bierregaard and Stouffer 1997, Oostra et al. 2008). In some cases fragmentation could increase the abundance and richness of some bird species (Azevedo-Ramos et al. 2006) as birds aggregate in the remaining available forests patches. This increase in abundance and richness is invariably followed by a steady reduction in diversity (Herkert 1994, Kruess and Tschardt 1994, Lida and Nakashizuka 1995), because the [available remaining](#) habitat is insufficient to sustain [either the increased abundance or](#) the large number of species (Fahrig 2003, Pimm and Askins 1995). Additionally, invasion of non-forest bird-species may increase competition for resources and increase parasite load, which in turn may further reduce the reproductive success and viability of populations within fragments (Christiansen and Pitter 1997, Duncan 1997).

Reductions in genetic variability, demographic crashes and higher susceptibility to catastrophic events have been hypothesized  resident bird populations in forest patches (Zuidema et al. 1996). These effects may be prevented if fragments are interconnected or connected [with to](#) larger continuous forests (Haddad et al. 2003, Uezu et al. 2005). Unfortunately, [due to given](#) species-specific differences in behavior, corridors are not suitable for all species (Rosenberg et al. 1997). Furthermore, newly fragmented habitats are often difficult to re-connect with larger forest fragments or with other small fragments; in most cases continuous habitats are impossible to recover. Hence, isolated forest patches often become the only species reservoirs of previously widespread avifaunas.

Northwestern Costa Rican dry-forest has been reduced to 0.1% of its original extension and the remaining forest consists of small patches surrounded by large cultivated areas (e.g., sugar cane, rice field, cattle haciendas) (Janzen 1988, Quesada and Stoner 2004). Consequently, the original terrestrial avifauna is now confined to these isolated, small forest patches; some of which are protected but with little, if any, chance of reconnection. As a first approach to [weigh estimate](#) the importance of these forest fragments for the dry forest avifauna, we tested the

effect of loss of natural habitat (Fahrig 2003, 2013) on species composition in dry forests of northwestern Costa Rica at two different levels: the entire bird community, and the assemblage of forest dependent species. We use nestedness analyses to test whether fragmentation or the length of the dry season (i. e., seasonality gradient) produce a nested species pattern. Testing if forest patches nest along a seasonal gradient provides information on the potential effect of climate changes predicted for the region (Sheffield and Wood 2008). A nested pattern is expected when species assemblages in species-poor sites are a subset of those assemblages present in species-rich sites (patch nestedness), or when species occupying few sites are a subset of those species occupying a large number of sites (species nestedness) (Novak *et al.* 2011). Hence nestedness may be the result of variation in rates of colonization and extinction among sites (Lomolino 1996), or among species (Atmar and Patterson 1993). We also test whether extinction (the likely cause of reduction of species across forest fragments) is caused by either a reduction in patch size, an increase in the distance between forest fragments as consequence of habitat deterioration, or if the nested pattern is associated with a climatic gradient (i.e., seasonality) (Lomolino 1996, Wright *et al.* 1998).

MATERIALS AND METHODS

Data collection

We gathered information on species composition from five forest fragments in northwestern Costa Rica that varied in size and connectivity (Table 1, Fig.1): Parque Nacional Diría (Dir), Reserva Natural Absoluta Cabo Blanco (CB), Parque Nacional Palo Verde and the Reserva Biológica Lomas Barbudal (PV), Parque Nacional Santa Rosa (SR), and Parque Nacional Rincón de la Vieja (RV). These forest patches are surrounded by large agricultural fields and human communities (Joyce 2006) and the distance between the nearest two forest patches included in this study is 58.9 km. There are some isolated trees and small tracts of early successional vegetation in the matrix that surround forest patches, but they are likely inadequate as corridors between patches. The fragmentation in the region has been the result of a progressive loss of natural habitats due to transformation of these habitats into agricultural fields (Boucher *et al.* 1983, Joyce 2006). We visited (GB, DO and JDRF) each site from 8 to 20 times to compile a comprehensive bird list of each site during the last 15 years, starting in 2002. We sampled 3-4 days during each visit and searched for birds from 8 to 12 walking hours/day. In sites in which access is difficult (e.g., RV) we extended the sampling period of each visit to 5-8 days, to reduce the number of visits. Particularly during the breeding period of most dry forest birds (May through July) we focused our efforts in detecting those elusive, rare species (e.g., some nightjars and cuckoos). We complemented our survey data with information from Stiles (1983), checklist

of SR and OTS (PV); Julio Sánchez and Luis Sandoval provided us additional data for PV and RV respectively.

Climatically the northwestern region of Costa Rica is characterized by a long dry season from December through May (Mata and Echeverría 2004) followed by a rainy season. However the local conditions affect the length of the dry season across sites (Sánchez-Murillo et al. 2013), and this makes it possible to order sites along a gradient of seasonality (Table 1). Precipitation patterns influence vegetation in the region, which is dominated by deciduous vegetation with evergreen species along rivers, and seasonal and permanent streams (Hartshorn 1983). We obtained the area of each patch, for statistical analyses, from the Sistema Nacional de Areas de Conservación de Costa Rica (<http://www.sinac.go.cr>). For PV we excluded the area covered by wetlands and included the area of the Reserva Biológica Lomas Barbudal because it is connected with PV, and excluded the area on the Caribbean slope of RV because this area is covered with rain forests rather than dry forests (Hartshorn 1983).

We excluded fresh water (e.g. Anatidae, Ardeidae) and marine birds (e.g. Fregatidae) from our analyses because they are restricted to habitats that are not present in all sites. We also excluded migratory birds. Occasional native species far from their normal geographic breeding distribution ranges were also excluded. Thus, the dry-forest bird-community was composed of resident, breeding species with terrestrial habits. Each bird species was classified into one of three forest dependency categories following Stiles (1985) with modifications by Sandoval and Barrantes (2009): 1 = species that live and reproduce in extensive mature forest; 2 = species that require habitats with 40-50% of forest cover; 3 = species that inhabit open areas. Species in categories 1 and 2 are likely more affected by habitat loss than those species included in category 3.

Statistical analyses

We ~~used a Sørensen Similarity Index to~~ evaluated similarity of bird species composition among sites ~~using Sorensen's Index,~~ and ~~assessed~~~~tested thefor a~~ relationship between species composition and geographic distances between sites using a Mantel test. We also determined whether composition of resident species across dry forest patches follows a nested distribution, or if each patch contains an independent subset of species, using the Vegan package (version 1.17; <http://cran.r-project.org>) implemented in the R Statistical Language (version 3.00; R Core Team 2015). A nested species distribution occurs when species richness in smaller fragments is a subset of the richness of larger fragments. To test for ~~species~~ nestedness in the ~~avifauna of~~ dry forest patches we used presence/absence matrices in which rows and columns were patches and species respectively, and then sorted rows (assemblages) and columns (species) by ~~two criteria: along~~ a gradient of patch sizes, and ~~along~~ a gradient of rainfall seasonality. ~~On these matrices w~~We calculated the NODF metric (Almeida-Neto *et al.* 2008, Ulrich *et al.* 2009, Moreira and Maltchik

2012) and used 999 permutations with the ‘quasiswap’ algorithm to estimate ~~the model-~~ probability (Miklós and Podani 2004) ~~by determining if that~~ the estimated nestedness differed from a random (non-nested) distribution. ~~quasiswap~~ retains both rows (sites) and columns (species) frequencies and does not increase Type I or Type II errors (Gainsbury and Colli 2003). We used the NODF metric because it independently estimates nestedness of species assemblages among sites (NODF rows), and nestedness for occupancy or presence among species (NODF columns), and for the entire matrix that we refer to as community (Almeida-Neto *et al.* 2008). NODF, for instance, calculates the nestedness of sites by comparing the occurrence of each species in each site (i.e. fill or empty cells) with the marginal values corresponding to all sites, and then ranking the sites by a previous determined gradient (e.g., area of fragments) (Almeida-Neto *et al.*, 2008). NODF is reported in values ranging from 0 (not nested) to 100 (maximum nestedness). These models do not incorporate the probability of detection of each species, but require that all (or nearly so) species from each fragment are included.

We also inferred whether nestedness was either caused by differential extinction due to a reduction in patch size or by rainfall seasonality (Cutler 1991, Lomolino 1996, Patterson 1990, Patterson and Atmar 1986) conducting the statistical analyses described by Lomolino (1996): $\%PN = 100 \times (R-D)/R$, where $\%PN$ = % of perfect nestedness, R = mean number of departures from random simulations, and D = number of species that depart from perfect nestedness. To estimate the probability associated with the D statistic, we took the ratio of species that depart from perfect nestedness, between the original matrix and those obtained from 999 randomly generated matrices (scripts for running these analyses are included as supplemental material). Lomolino’s statistics were calculated for presence/absence species matrix in which sites were first ordered by decreasing area and then along a gradient of seasonality (Fig. 1). Analyses were conducted for all the species and for forest dependent species (categories 1 and 2 of forest dependence). With these matrices we tested if nestedness is caused by differential extinction due to area reduction or rainfall seasonality.

RESULTS

We registered a total of 187 resident species in all study sites (Table S1). PV had the most resident species while CB and Dir had the fewest, but the number of species did not differ significantly across sites ($\chi^2 = 5.51$, $df = 4$, $p = 0.239$; Table 1). RV was least similar in species composition with all other sites, and CB and Dir were most similar (Table 2). Species richness was independent of both geographic distance (Mantel test = 0.42, $p = 0.185$; Table 2) and fragment area ($r = 0.41$, $p = 0.494$).

Patch size and rainfall were not correlated (Spearman = 0.70, $p = 0.180$), but both factors affected similarly the nested pattern at three different levels: bird community (entire matrix), bird

assemblages, and species occurrence among dry forest patches. The community was significantly nested based on overlap and decreasing fill statistics - NODF) by size of dry forest patches (NODF = 31.6, $p = 0.001$). Furthermore, species occupancy was nested among patches (NODF columns = 31.6, $p = 0.001$), but bird assemblages were not nested by size of patches (NODF rows = 65.6, $p = 0.099$), though this probability may imply nestedness, with the possibility of an outlier. The entire community also nested within forests ranked by length of dry season (NODF = 31.6, $p = 0.001$). The bird assemblages showed a weak tendency to be nested in patches ordered along this gradient of rainfall seasonality (NODF rows = 32.0, $0.05 < p < 0.1$) and species occupancy was strongly nested along such gradient (NODF columns = 31.6, $p = 0.001$). The similarity of these results indicate that both factors affected the nestedness of species in dry forest patches, but the small sample size ($N = \text{five patches}$) preclude prevent us to from testing the interaction of both factors on species nestedness.

The subset of forest dependent species (categories 1 and 2) was nested when considering area (NODF = 24.17, $p = 0.001$) or seasonality (NODF = 24.15, $p = 0.001$) of dry forest fragments. Bird assemblages of forest dependent species nested among forest fragments ranked along a seasonality gradient (NODF rows = 42.15, $p = 0.005$), but not by area of fragments (NODF rows = 57.68, $p = 0.397$). The species occupancy nested along both gradients: seasonality (NODF columns = 24.13, $p = 0.001$) and area (NODF columns = 24.13, $p = 0.001$). According to Lomolino's test, differential extinction for the entire community was not due to habitat loss ($D = 121$, $R = 127.9$, $p = 0.386$, %PN = 6.9), distance between fragments ($D = 120$, $R = 128.9$, $p = 0.336$, %PN = 6.9), nor rainfall seasonality ($D = 118$, $R = 128.7$, $p = 0.276$, %PN = 8.3). Results are similar for forest dependent species (Table S2).

In general the proportion of species included in the three categories of forest dependency was similar for all sites ($\chi^2 = 7.7$, $df = 8$, $p = 0.468$; Table 3). The number of forest dependent species (category 1) did not differ across sites ($\chi^2 = 5.1$, $df = 4$, $p = 0.167$; Table 3). From this category 18 species were detected in only one site and 72% of them were exclusively detected in RV (Table 3). Similarly, for species in the category 2 we detected 58% only in RV. From the category 3 only four species were detected in only one site.

DISCUSSION

Area did not explain the number of species found in these forest patches. This suggests that other factors, such as environmental heterogeneity may also influence the number and/or composition of species in fragments. For instance, patches with complex topography (e.g., altitudinal gradient, mountains) often have higher species richness, or at least a different subset of species when compared with patches with relatively homogeneous topographies (Primack 1998, Fernández-Juricic 2000, Mayr and Diamond 2001). The characteristics of the matrix surrounding

fragments, connectivity between fragments, edge effect, and human interventions may also influence species richness within fragments (Bierregaard and Stouffer 1997, Whitmore 1997).

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

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

Species composition across sites may be related to vegetation features than to area of fragments or geographic isolation. The area of the patches included in this study does not predict the number of species present in each fragment. For instance, Santa Rosa nearly triples the area of PV, but they both have similar species richness. Likewise, CB has only one fifth the area of Dir, but the number of species is similar in both sites. SR and Palo Verde are primarily deciduous forest and small tracts of evergreen vegetation (Hartshorn 1983) and both sites have a similar species composition. Dir and CB share also a high percentage of species and both have more humid conditions than SR and PV and larger tracts of evergreen forest, as a result of a shorter dry season (Janzen 1986, Sánchez-Murillo *et al.* 2013). On the contrary, RV shares fewer species with other dry forest patches, and populations of many of these species are well isolated by

topographic barriers from other populations (Barrantes 2009, Barrantes et al. 2011). The topography of RV is more complex and includes an altitudinal gradient covered by forests with different structure (Janzen 1986). The differences in species composition across sites highlight two important aspects: first that species composition should be analyzed at a finer scale taking forest structure and composition into account; and second, that to preserve the rich dry forest avifauna it is necessary to preserve ecosystem diversity, e.g., through habitat restoration and fragments connection.

Results in Table 3 indicate that between 5.3 to 11.8% of all native species in dry forest patches require large areas of mature forests and more than 40% of the species in each forest patch require at least 50% of forest cover for feeding and reproduction (Stiles 1985). Hence, forest patches in northwestern Costa Rica support a large number of species that require large tracts of mature tropical dry forests in the most threaten forest ecosystem in Mesoamerica (Janzen 1988). These patches are then an important reservoir for the rich dry forest Mesoamerican avifauna (Stotz *et al.* 1996), including four endemic species to the Pacific slope of Middle America dry forest region (Lesser Ground Cuckoo, Pacific Screech Owl, Long Tailed Manakin, White Throated Magpie-Jay), but habitat destruction, the removal of isolated trees and forest patches reduces connectivity and may drastically reduce the viability of populations in remnant forest fragments. In these isolated small patches genetic variability may decrease rapidly (Evans and Sheldon 2008, but see Fuchs and Hamrick 2010) and the recurrent catastrophic events caused primarily by intentional fires (Quesada and Stoner 2004) seriously threaten the long-term maintenance of bird populations.

—In conclusion, forest patches in northwestern Costa Rica are reservoirs of a large portion of bird species of the Pacific slope of Central American dry forests. However, species composition varies widely across fragments possibly as a consequence of differences in vegetation, climatic and topographic conditions. In northwestern Costa Rica, the reduction of the original dry forest into small, isolated patches resulted in a nested pattern of both bird assemblages and species. The lack of connectivity between these fragments and the recurrent intentional fires in the region, and the predicted global climatic changes threaten the long-term population-viability of many bird species. Nestedness analyses proved to be an important tool to evaluate the consequences of habitat loss of natural environments. Most importantly, this method can be used periodically to evaluate the effect of changes in climate and land use on the avifauna (or other animals) in forest patches.

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REFERENCES

294 Almeida-Neto, M., P. Guimarães, P. R. Guimarães Jr., R. D. Loyola and W. Ulrich. 2008. A
 295 consistent metric for nestedness analysis in ecological systems: reconciling concept and
 296 measurement. *Oikos* 117: 1227–1239.

297 Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a
 298 landscape perspective. *Ecology* 73: 794–804.

299 Atmar, W. and B. D. Patterson. 1993. The measure of order and disorder in distribution of species
 300 in fragmented habitats. *Oecologia* 96: 373–382.

301 Azevedo-Ramos, C., O. de Carvalho Jr. and B. D. do Amaral. 2006. Short-term effects of
 302 reduced-impact logging on eastern Amazon fauna. *Forest Ecology and Management* 232:
 303 26–35.

304

305 Barlow, J. and C. A. Peres. 2004. Ecological responses to El Niño–induced surface fires in central
 306 Brazilian Amazonia: management implications for flammable tropical forests. *Philosophical*
 307 *Transactions of the Royal Society B* 359: 367–380.

308 Barrantes, G. 2009. The role of historical and local factors in determining species composition of
 309 the highland avifauna of Costa Rica and western Panamá. *Revista Biología Tropical* 57
 310 (Suppl. 1): 323–332.

311 Barrantes, G. and J. E. Sánchez. 2004. Geographical distribution, ecology, and conservation
 312 status of costa rican dry-forest avifauna. Pp. 147–159. In: Frankie G. W., A. Mata and S. B.
 313 Vinson (eds). *Biodiversity Conservation in Costa Rica*. University of California press,
 314 Berkeley, California.

315 Barrantes, G., M. Iglesias and E. J. Fuchs. 2011. The roles of history and habitat area on the
 316 distribution and composition of avian species assemblages in the highlands of Costa Rica.
 317 *Journal of Tropical Ecology* 27:1–8.

318 Bierregaard, Jr. R. O. and P. C. Stouffer. 1997. Understory birds and dynamic habitat mosaics in
 319 Amazonian rainforests. Pp. 138–155. In, Laurance W. F. and R. O. Bierregaard, Jr. (eds.).
 320 *Tropical forest remnants. Ecology, management, and conservation of fragmented*
 321 *communities*. University of Chicago press, Chicago, Illinois.

322 Boucher, D. H., M. Hansen, S. Risch, and J. H. Vandermeer. 1983. Agriculture. Pp. 66–73. In:
 323 Janzen, D. H. (ed). *Costa Rican Natural History*. Chicago University press, Chicago,
 324 Illinois.

325 Cai, W., S. Borlace, M. Lengaigne, P. van Rensch, M. Collins, G. Vecchi, A. Timmermann, A.
 326 Santoso, M. J. McPhaden, L. Wu, M. H. England, G. Wang, E. Guilyardi and F.-F. Jin.
 327 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature*
 328 *Climate Change* 4, DOI: 10.1038/NCLIMATE 2100

329 Christiansen, M. B. and E. Pitter. 1997. Species loss in a forest bird community near Lagoa Santa
 330 in southeastern Brazil. *Biological Conservation* 80: 23–32.

331 Cutler, A. 1991. Nested faunas and extinction in fragmented habitats. *Conservation Biology* 5:
332 496–504.

333 Duncan, R. P. 1997. The role of competition and introduction effort in the success of Passeriform
334 birds introduced to New Zealand. *American Naturalist* 149: 903–915.

335 Evans, S. R. and B. C. Sheldon. 2008. Interspecific patterns of genetic diversity in birds:
336 correlations with extinction risk. *Conservation Biology* 22: 1016–1025.

337 Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology,*
338 *Evolution, and Systematics* 34: 487–515.

339 Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis.
340 *Journal of Biogeography* 40: 1649–1663.

341 Fernández-Juricic, E. 2000. Bird community composition patterns in urban parks of Madrid: the
342 role of age, size and isolation. *Ecological Research* 15: 373–383.

343 Fuchs, E. J. and J. L. Hamrick. 2010. Genetic diversity in the endangered tropical tree,
344 *Guaiacum sanctum* (Zygophyllaceae). *Journal of Heredity* 101: 284–291.

345 Gainsbury, A. M. and G. R. Colli. 2003. Lizards assemblages from natural Cerrado enclaves in
346 southwestern Amazonia: the role of stochastic extinctions and isolation. *Biotropica* 35:
347 503–519.

348 Graham, C. H. and J. G. Blake. 2001. Influence of patch- and landscape-level factors on Bbrd
349 assemblages in a fragmented tropical landscape. *Ecological Applications* 11: 1709–1721.

350 Haddad, N. M., D. R. Bowne, A. Cunningham, B. J. Danielson, D. J. Levey, S. Sargent, and T.
351 Spira. 2003. Corridor use by diverse taxa. *Ecology* 84: 609–615

352 Hartshorn, G. S. 1983. Plants. Pp. 118–183. In: Janzen, D. H. (ed). *Costa Rican Natural*
353 *History*. Chicago University press, Chicago, Illinois.

354 Harvey, C. A., C. Villanueva, J. Villacís, M. Chacón, D. Muñoz, M. López, M. Ibrahim, R.
355 Gómez, R. Taylor, J. Martinez, A. Navas, J. Saenz, D. Sánchez, A. Medina, S. Vilchez, B.
356 Hernández, A. Perez, F. Ruiz, F. López, I. Lang and F. L. Sinclair. 2005. Contribution of
357 live fences to the ecological integrity of agricultural landscapes. *Agriculture, Ecosystems*
358 *and Environment* 111: 200–230

359 Herkert J. R. 1994. The effects of habitat fragmentation on Midwestern grassland bird
360 communities. *Ecological Applications* 4: 461–471.

361 Jaeger, J. A. G. 2000. Landscape division, splitting index, and effective mesh size: new measures
362 of landscape fragmentation. *Landscape Ecology* 15: 115–130.

363 Janzen, D. H. 1986. Guanacaste National Park: tropical ecological and cultural restoration.
364 Editorial Universidad Estatal a Distancia. 103 p.

365 Janzen, D. H. 1988. Tropical dry forest: the most endangered mayor tropical ecosystem. Pp. 130–
366 137. In: Wilson, E. O. (ed). *Biodiversity*. National Academy Press, Washington D. C.

367 Joyce, A. T. 2006. Land use change in Costa Rica: 1996–2006, as influenced by social, economic,
368 political, and environmental factors. Litografía e imprenta LIL, S.A., San José, Costa Rica.
369 276 p.

370 Kruess A. and T. Tschardtke. 1994. Habitat fragmentation, species loss, and biological control.
371 Science 264: 1581–1584.

372 Lambin, E. F., H. J. Geist, and E. Lepers 2003. Dynamics of land-use and land-cover change in
373 tropical regions. Annual Review of Environment and Resources. 28: 205–241.

374 Lida, S. and T. Nakashizuka. 1995. Forest fragmentation and its effect on species diversity in sub-
375 urban coppice forests in Japan. Forest Ecology and Management 73: 197–210.

376 Lomolino, M. V. 1996. Investigating causality of nestedness of insular communities: selective
377 immigrations or extinctions? Journal of Biogeography 23: 699–703.

378 Martínez, M. L., O. Pérez-Maqueo, G. Vázquez, G. Castillo-Campos, J. García-Franco, K.
379 Mehlreter, M. Equihua, and R. Landgrave. 2009. Effects of land use change on
380 biodiversity and ecosystem services in tropical montane cloud forests of Mexico. Forest
381 Ecology and Management 258: 1856–1863.

382 Mata, A. and J. Echeverría. 2004. Introduction. Pp. 1–12. In: Frankie G. W., A. Mata and S. B.
383 Vinson (eds). Biodiversity Conservation in Costa Rica. University of California press,
384 Berkeley, California.

385 Mayr, E. and J. Diamond. 2001. The birds of northern Melanesia. Oxford University press, New
386 York. 492 p.

387 Miklós, I. and J. Podani. 2004. Randomization of presence-absence matrices: comments and new
388 algorithms. Ecology 85: 86–92.

389 Moreira, L. F. and L. Maltchik. 2012. Assessing patterns of nestedness and co-occurrence in
390 coastal pond anuran assemblages. Amphibia-Reptilia 33: 261–271.

391 Novak, M., J. W. Moore and R. A. Leidy. 2011. Nestedness patterns and the dual nature of
392 community reassembly in California streams: a multivariate permutation-based approach.
393 Global Change Biology 17: 3714–3723.

394 Oostra V., L. G. L. Gomes and V. Nijman. 2008. Implications of deforestation for the abundance
395 of restricted-range bird species in a Costa Rican cloud-forest. Bird Conservation
396 International 18: 11–19.

397 Patterson, B. D. 1990. On the temporal development of nested subset patterns of species
398 composition. Oikos 59: 330–342.

399 Patterson, B. D. and W. Atmar. 1986. Nested subsets and the structure of insular mammalian
400 faunas and archipelagos. Biological Journal of the Linnean Society 28: 65–82.

401 Pimm S. L. and R. A. Askins. 1995. Forest losses predict bird extinctions in eastern North
402 America. Proceedings of the National Academy of Science 92: 9343–9347.

403 Primack, R. B. 1998. Essentials of conservation biology. Sinauer Associates, Sunderland,
 404 Massachusetts. 659 p.
 405 Quesada, M. and K. E. Stoner. 2004. Threads to the conservation of tropical dry forest in Costa
 406 Rica. Pp. 266–280. In: Frankie G. W., A. Mata and S. B. Vinson (eds). Biodiversity
 407 Conservation in Costa Rica. University of California press, Berkeley, California.
 408 R DEVELOPMENT CORE TEAM. 2013. R: a language and environment for statistical
 409 computing. R Foundation for Statistical Computing, Vienna, Austria. [http://www.R-](http://www.R-project.org/)
 410 [project.org/](http://www.R-project.org/)
 411 Renjifo, L. M. 2001. Effect of natural and anthropogenic landscape matrices on the abundance of
 412 subandean bird species. Ecological Applications 11: 14–31.
 413 Rosenberg D. K., B. R. Noon and E. C. Meslow. 1997. Biological corridors: form, function, and
 414 efficacy. BioScience 47: 677–687.
 415 Sánchez-Murillo, R., G. Esquivel-Hernández, K. Welsh, E. S. Brooks, J. Boll, R. Alfaro-Solís, J.
 416 Valdés-González. 2013. Spatial and Temporal Variation of Stable Isotopes in Precipitation
 417 across Costa Rica: An Analysis of Historic GNIP Records. Open Journal of Modern
 418 Hydrology 3: 226-240.
 419 Sandoval, L. and G. Barrantes. 2009. Relationship between species richness of excavator birds
 420 and cavity-adopters in seven tropical forests in Costa Rica. Wilson Bulletin 121: 75–81.
 421 Sheffield, J. and E. F. Wood. 2008. Projected changes in drought occurrence under future global
 422 warming from multi-model, multi-scenario, IPCC AR4 simulations. Climate Dynamics 31:
 423 79–105.
 424 Stiles, F. G. 1983. Checklist of birds. Pp. 530–544. In: Janzen, D. H. (ed). Costa Rican Natural
 425 History. Chicago University press, Chicago, Illinois.
 426
 427 Stiles, F. G. 1985. Conservation of forest birds of Costa Rica: problems and perspectives. Pp.
 428 121–138. In: Diamond A. W. and Lovejoy T. S. (eds). Conservation of tropical forest
 429 birds. Technical Publication Number 4, International Council for Bird Preservation,
 430 Cambridge, United Kingdom.
 431 Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III and D. K. Moskovits. 1996. Neotropical birds.
 432 Ecology and conservation. University of Chicago Press, Chicago, IL. 478 p.
 433 Uezu, A., J. P. Metzger, and J. M. E. Vielliard. 2005. Effects of structural and functional
 434 connectivity and patch size on the abundance of seven Atlantic Forest bird species.
 435 Biological Conservation 123: 507–519.
 436 Ulrich, W., M. Almeida-Neto and N. J. Gotelli. 2009. A consumer's guide to nestedness analysis.
 437 Oikos 118: 3–17.
 438 Whitmore, T. C. 1997. The tropical forest disturbance, disappearance, and species loss. Pp. 3-12.
 439 In, Laurance W. F. and R. O. Bierregaard, Jr. (eds.). Tropical forest remnants. Ecology,

440 management, and conservation of fragmented communities. University of Chicago press,
 441 Chicago, Illinois.

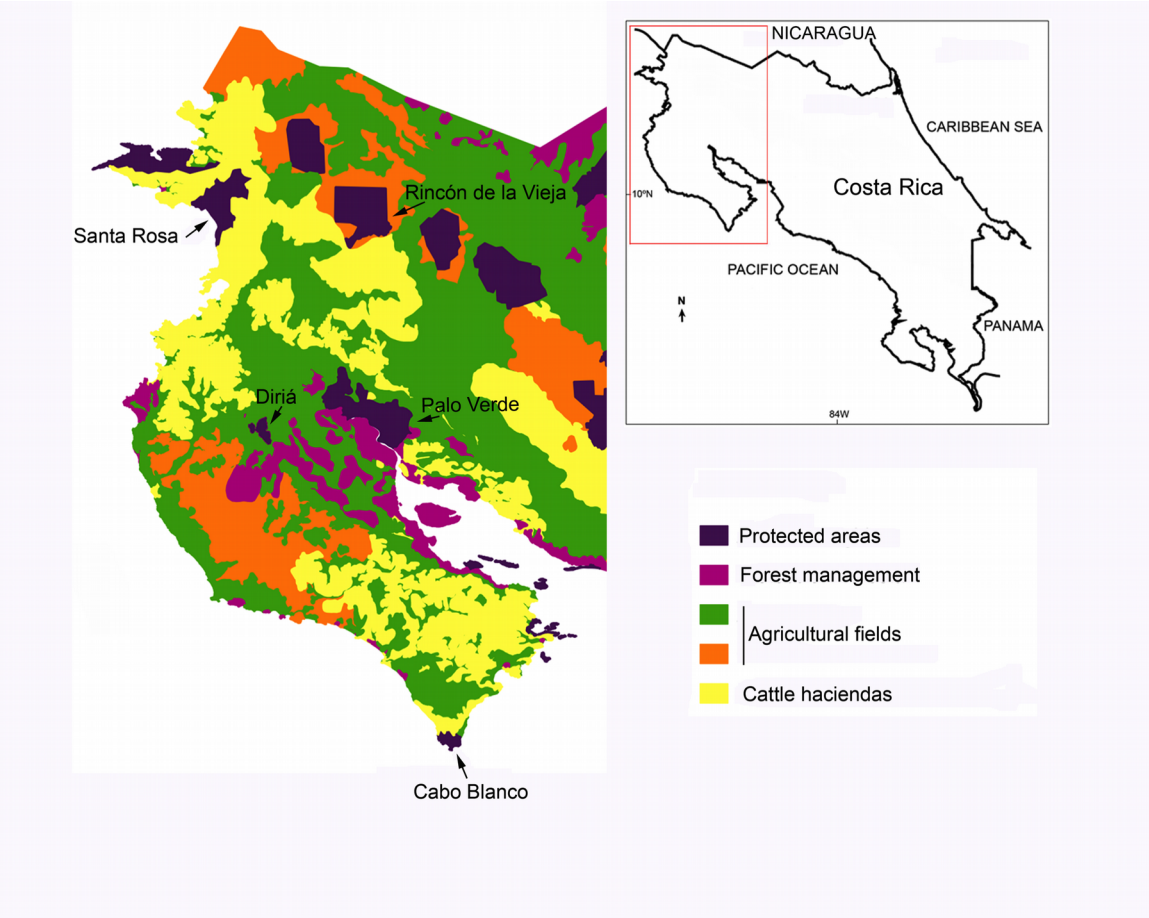
442 Wright, D. H., B. D. Patterson, G. M. Mikkelsen, A. Cutler and W. Atmar. 1998. A comparative
 443 analysis of nested subset patterns of species composition. *Oecologia* 113:1–20.

444 Zuidema P.A., J. Sayerand and W. Dijkman. 1996. Forest fragmentation and biodiversity: the case
 445 for intermediate-sized reserves. *Environmental Conservation* 2: 290–297.

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Fig.1. Dry forest fragments and areas with different use in northwestern Costa Rica. The inset shows the map of Costa Rica.



454 Table 1. Area, location and number of native species recorded in five dry forest fragments in
 455 northwestern Costa Rica. Dry season includes the length of dry season in months and is based on
 456 meteorological stations located in the same or nearby sites.

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Locality	Dry season	Area (ha)	Location	No. of species
Santa Rosa	6-6.5	37117	10°50'N, 85°37'W	123
Palo Verde	5-5.5	11970	10°20'N, 85°20'W	135
Rincón de la Vieja	2-3	8411	10°49'N, 85°21'W	127
Diriá	4.5-5	5426	10°10'N, 85°35'W	109
Cabo Blanco	3-4	1172	09°33'N, 85°06'W	104

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Table 2. Sørensen similarity index and the number of species shared between sites in parentheses (below the diagonal) and distance (km) (above the diagonal) between five forest patches in northwestern Costa Rica. **HigherLarger** values of the Sørensen similarity index indicate **highergreater** similarity in species composition between sites.

	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)

Table 3. Species included in each category of forest dependence. The first row includes the total number of species in each category and the number of species detected in a single sampling site. The other rows include the number of species of that particular category detected in each site and the number of species detected only in that particular site. The percentage of restricted species of each category per site is shown in parenthesis.

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)