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 were nested within patches ordered by a gradient of seasonality, and only occupancy of species was nested by area of patches. Thus, forest patches with a shorter dry season include more forest dependent species.

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

INTRODUCTION

Deforestation and change in land use are the primary factors causing habitat degradation and forest fragmentation in tropical regions (Jaeger 2000, Lambinet al. 2003, Azevedo-Ramos *et al.* 2006, Joyce 2006, Martínez et al. 2009). These changes in natural landscapes may often reduce connectivity for species trying to move between fragments embedded in a matrix that consists of anthropogenic and semi-natural habitats (Renjifo 2001, Graham and Blake 2001). Additionally, the negative effects of habitat fragmentation may be exacerbated by increased predation and competition within habitat patches (Andrén 1992, Fahrig 2003). Thus, the direct and indirect negative effects of habitat 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 bird species richness and the abundance of bird species (Azevedo-Ramos *et al.* 2006) as birds aggregate in the remaining available forests patches. But this increase is invariably followed by a steady reduction (Herkert 1994, Kruess and Tscharntke 1994, Lida and Nakashizuka 1995), because the remaining habitat is insufficient to sustain either the increased abundance or a large number of species (Fahrig 2003, Pimm andAskins 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 for resident bird populations in forest patches (Zuidema *et al*. 1996). These effects may be prevented if fragments are interconnected or connected to larger continuous forests (Haddad et al. 2003, Uezu et al. 2005). Unfortunately, due to 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 a series of small patches surrounded by large cultivated areas (e.g., sugar cane, rice field, cattle haciendas; Quesada and Stoner 2004) which cover only 0.1% of its original extension (Janzen 1988). 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 estimate the importance of these forest fragments for the dry forest avifauna, we tested the effect of natural habitat fragmentation (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. Most dry forest birds occupied originally nearly the entire northwestern region of Costa Rica, and even species that now occur at middle elevations were reported at lower elevations (Wetmore 1944, Slud 1980). Thus, it is likely that the distribution of most species has been affected by fragmentation due to habitat loss. 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 species richness reduction 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 Diriá (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 fragmentation than those species included in category 3.

Statistical analyses

We evaluated similarity of bird species composition among sites using Sørensen Index and tested for 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 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 a gradient of patch sizes, and a gradient of rainfall seasonality. 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 construct a null distribution of NODF values (Miklós and Podani 2004). During each permutation the 'quasiswap' algorithm randomly shuffles values of rows and columns but maintains constant marginal frequencies (total frequencies of rows and columns). We then estimated the probability that the calculated nestedness differed significantly from the generated null distribution-. 'Quasiswap' in addition to retaining row (sites) and column (species) frequencies, 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 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 x (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 a 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 extinction due to area reduction or rainfall seasonality.

RESULTS

We registered a total of 187resident 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 ($x^2 = 5.51$, 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 value of NODF (overlap and decreasing fill statistics) indicated that the community was significantly nested 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 (Fig. 2), but the small sample size (N = five patches) prevented us 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, reduction in species richness 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 (x^2= 7.7, df = 8, p = 0.468; Table 3). The number of forest dependent species (category 1) did not differ across sites (x^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, which ~~. This~~ suggests that other factors, such as environmental heterogeneity, ~~may also~~ influenced 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 (Fig. 2). 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.

Fragmentation did not appear to cause a reduction in species richness (based on Lomolinos' test) among forest patches. In systems in which nestedness is caused by the interaction of different factors, as ~~it~~ seems to be the case ~~in this study~~here, Lomolinos' test is likely to fail~~s~~ to detect the causes of nestedness. This test has several assumptions (e.g., correlation between nestedness and area of fragments, extinctions are not correlated with isolation) and ~~biases in these~~incorrect assumptions may ~~likely affect~~influence its sensitivity (Lomolino 1996). In this study, several factors may obscure the signature of habitat fragmentation (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., *Callocitta 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 more 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, while having similar species richness, SR is nearly three times~~triples~~ the area of PV~~, but they both have similar species~~

~~richness~~. Likewise, species richness is similar in CB and Dir, but the area of CB ~~ha~~is only ~~one-fifth~~20% of the area of Dir~~, but the number of species is similar in both sites~~. SR and PV are primarily deciduous forest and small tracts of evergreen vegetation (Hartshorn 1983) and both sites have ~~a~~ similar species compositions. Dir and CB share ~~also a high percentage of~~many 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 to 12% 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 reduce 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 fragmentation of natural environments. Most important, this method can be used periodically to evaluate the effect of changes in climate and land use on the avifuna (or other animals) in forest patches.

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REFERENCES

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

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

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

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

Barlow, J. and C. A. Peres. 2004. Ecological responses to El Niño–induced surface fires in central Brazilian Amazonia: management implications for flammable tropical forests. Philosophical Transactions of the Royal Society B359: 367–380.

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

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

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

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

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

Cai, W., S. Borlace, M. Lengaigne, P. van Rensch, M. Collins, G. Vecchi, A. Timmermann, A. Santoso, M. J. McPhaden, L. Wu, M. H. England, G. Wang, E. Guilyardi and F.-F. Jin. 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. Nature Climate Change 14, DOI: 10.1038/ NCLIMATE 2100

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

Cutler, A. 1991.Nested faunas and extinction in fragmented habitats. Conservation Biology5: 496–504.

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

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

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

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

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

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

Gainsbury, A. M. and G. R. Colli. 2003. Lizards assemblages from natural Cerrado enclaves in southwestern Amazonia: the role of stochastic extinctions and isolation. Biotropica35: 503–519.

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

Haddad, N. M., D. R. Bowne, A. Cunningham, B. J. Danielson, D. J. Levey, S. Sargent, and T. Spira. 2003. Corridor use by diverse taxa. Ecology84: 609–615

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

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

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

Jaeger, J. A. G. 2000. Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Landscape Ecology15: 115–130.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Patterson, B. D. and W. Atmar. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. Biological Journal of the Linnean Society28: 65–82.

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

Primack, R. B. 1998.Essentials of conservation biology. Sinauer Associates, Sunderland, Massachusetts. 659 p.

Quesada, M. and K. E. Stoner. 2004. Threads to the conservation of tropical dry forest in Costa Rica. Pp. 266–280. In: Frankie G. W., A. Mata and S. B. Vinson (eds). Biodiversity Conservation in Costa Rica. University of California press, Berkeley, California.

R DEVELOPMENT CORE TEAM.2013. R: a language and environment for statistical computing. R Foundation for StatisticalComputing, Vienna, Austria.http://www.R-project.org/

Renjifo, L. M. 2001. Effect of natural and anthropogenic landscape matrices on the abundance of subandean bird species. Ecological Applications 11: 14–31.

Rosenberg D. K., B. R. Noon and E. C. Meslow. 1997. Biological corridors: form, function, and efficacy. BioScience 47: 677–687.

Sánchez-Murillo, R., G. Esquivel-Hernández, K. Welsh, E. S. Brooks, J. Boll, R. Alfaro-Solís, J. Valdés-González. 2013. Spatial and Temporal Variation of Stable Isotopes in Precipitation across Costa Rica: An Analysis of Historic GNIP Records. Open Journal of Modern Hydrology 3: 226-240.

Sandoval, L. and G. Barrantes. 2009. Relationship between species richness of excavator birds and cavity-adopters in seven tropical forests in Costa Rica. Wilson Bulletin 121: 75–81.

Sheffield, J. and E. F. Wood. 2008.– Projected changes in drought occurrence under future global warming from multi-model, multi-scenario, IPCC AR4 simulations. Climate Dynamics 31: 79–105.

Slud, P. 1980. The birds of hacienda Palo Verde, Guanacaste, Costa Rica. Smithsonian Contribution to Zoology 292: 1–92.

Stiles, F. G. 1983.Checklist of birds. Pp. 530–544. In: Janzen, D. H. (ed). Costa Rican Natural History. Chicago University press, Chicago, Illinois.

Stiles, F. G. 1985. Conservation of forest birds of Costa Rica: problems and perspectives. Pp. 121–138. In: Diamond A. W. and Lovejoy T. S. (eds). Conservation of tropical forest birds.

Technical Publication Number 4, International Council for Bird Preservation, Cambridge, United Kingdom.

Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III and D. K. Moskovits. 1996. Neotropical birds. Ecology and conservation. University of Chicago Press, Chicago, IL. 478 p.

Uezu, A., J. P. Metzger, and J. M. E. Vielliard. 2005. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. Biological Conservation 123: 507–519.

Ulrich, W., M. Almeida-Neto and N. J. Gotelli. 2009. A consumer’s guide to nestedness analysis. Oikos 118: 3–17.

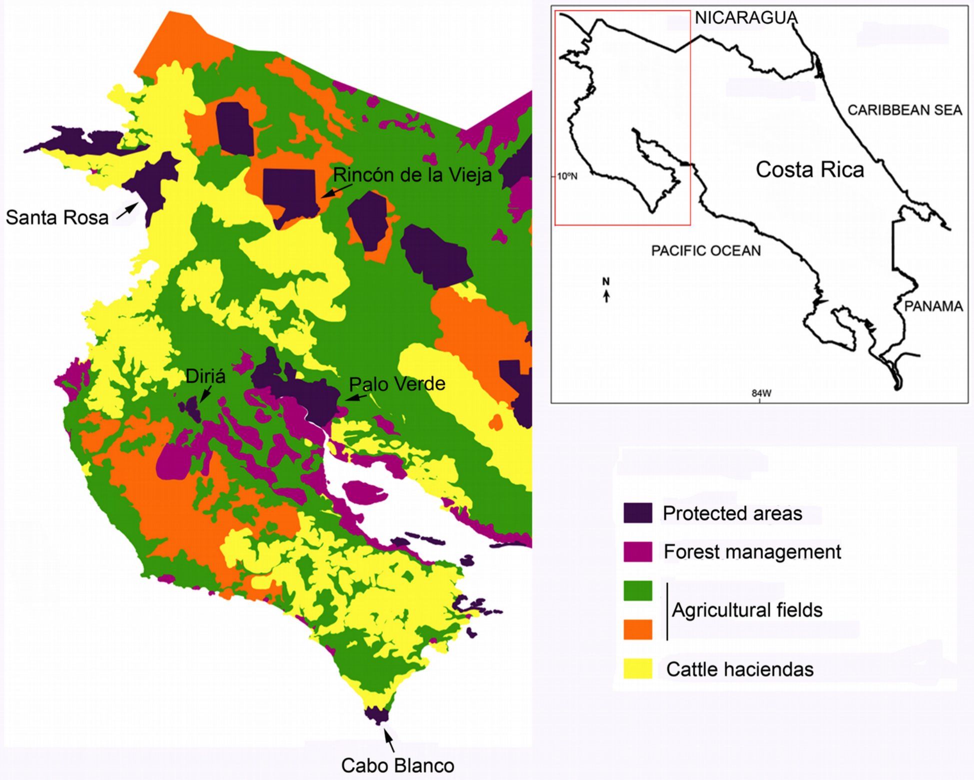
Whitmore, T. C. 1997.The tropical forest disturbance, disapperance, and species loss. Pp. 3-12. In, Laurance W. F. and R. O. Bierregaard, Jr. (eds.). Tropical forest remnants. Ecology, management, and conservation of fragmented communities. University of Chicago press, Chicago, Illinois.

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

Wetmore, A. 1944. A collection of birds from northern Guanacaste, Costa Rica. Proceedings of the United States National Museum 95: 25–80.

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

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



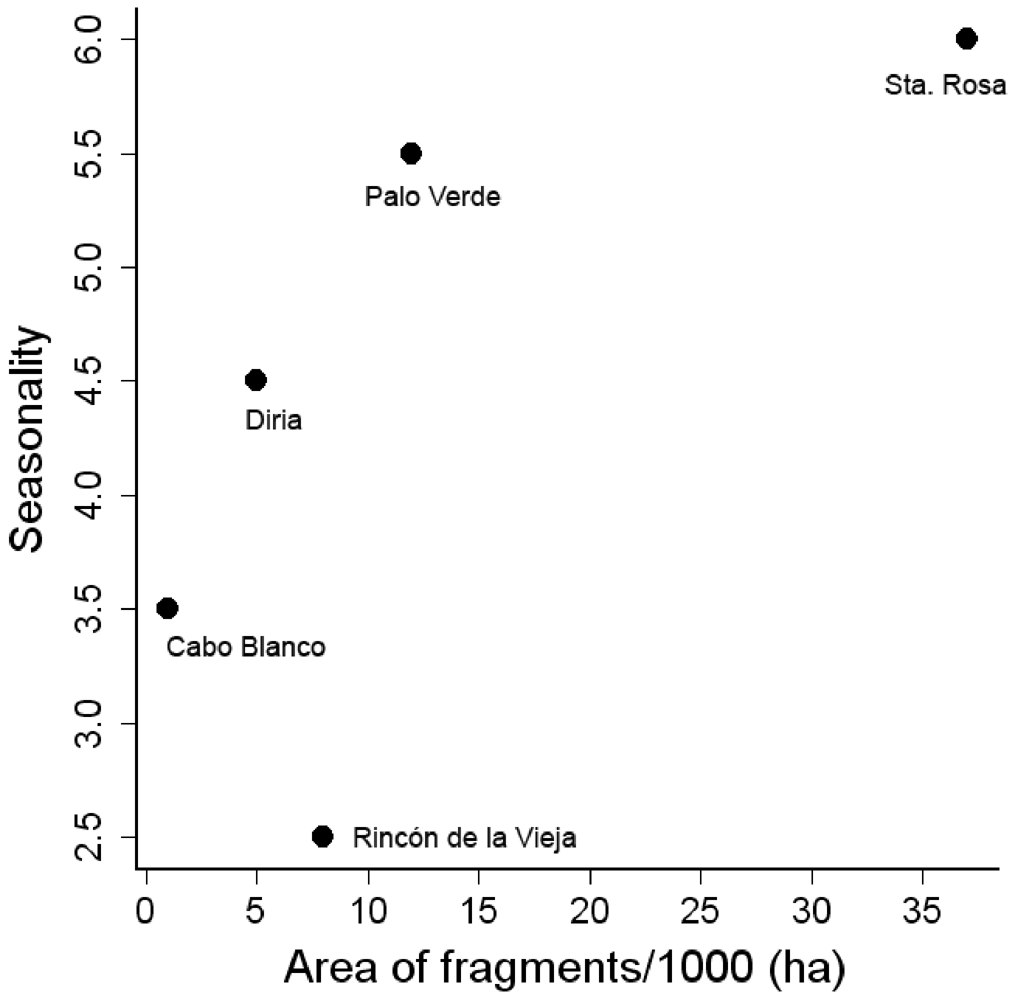


Fig. 2. Relationship between area of fragments and seasonality, estimated as the length of dry season in months.

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

Locality	Dry season	Area (ha)	Location	No. ofspecies
Santa Rosa	6-6.5	37117	10º50’N, 85º37’W	123
Palo Verde	5-5.5	11970	10º20’N, 85º20’W	135
Rincón de laVieja	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

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. Larger values of the Sørensen similarity index indicate greater 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.

	Category 1		Category 2		Category 3	
Site	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