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Abstract: Deforestation and land use change have reduced the tropical dry forest in ~~the~~ northwestern ~~region of~~ Costa Rica into isolated fragments. We examined the effect of fragment area and length of the dry season (seasonality) on nestedness ~~for~~ the community (entire species matrix), assemblages (forest fragments), and species occupancy across fragments for the native avifauna, and for a subset of forest dependent species. Area or distance between fragments did not correlate with species richness across fragments. Similarity in bird community composition between fragments was related with habitat structure; fragments with similar forest structure have higher similarity in their avifaunas. Fragment area determined the pattern of nestedness of the bird community and species occupancy, but not the nestedness of assemblages across fragments in northwestern Costa Rican avifauna. Forest dependent species (species that require large tracts of mature forest) and assemblages of these species were nested along forest fragments ranked by seasonality gradient, but only occupancy of species nested by fragment area.

Key words: Forest fragments, bird composition, nested community analysis, community similarity.

Deforestation and changes in land use are the main proximate factors causing habitat deterioration and forest fragmentation in tropical regions (Jaeger 2000, Azevedo-Ramos *et al.* 2006, Joyce 2006). These activities transform continuous forests into a collection of poorly interconnected small fragments, distantly separated from larger continuous forests (Harris 1988, Daily *et al.* 2001). Fragmentation changes environmental conditions within fragments resulting in a cascade of effects, typically starting with ~~an~~ ~~increasing~~ mortality of forest plant species (Kapos *et al*. 1997). Isolation may also reduce seedling establishment and affect pollination and seed dispersal rates (Murcia 1995, Fuchs *et al*. 2003). Environmental changes at the edge of fragments may also favor invasion and establishment of non-forest species, which may change the composition of fragments and increase~~s~~ predation rates as non-forest predators enter forest fragments (Andren and Angelstam 1988).

Bird communities undergo notable changes in composition and abundance soon after large forests are reduced into smaller fragments (Oostra *et al.* 2008[illegible]n 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 Tscharntke 1994, Lida and Nakashizuka 1995), because the available habitat is insufficient to sustain a 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 Pittier 1997, Duncan 1997).

Reduction of genetic variability, demographic crashes and higher susceptibility to catastrophic events are also expected for resident bird populations in forest fragments (Zuidema *et al*. 1996). These effects may be prevented if fragments are interconnected or connected with larger continuous forests. Unfortunately, given species-specific differences in behavior, corridors usually 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 fragments often become the only species reservoirs of previously widely spread and interconnected avifaunas.

Northwestern Costa Rican dry-forest has been reduced to 0.1% of its original extension and the remaining forest consists of small fragments 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 the importance of these forest fragments for the dry forest avifauna, we evaluate the effect of forest fragmentation on species composition for the bird community, but give special attention to forest dependant species in dry-forest fragments of northwestern Costa Rica. We use nestedness analyses to evaluate whether fragmentation or the length of the dry season (i. e., seasonality gradient) produce a nested species pattern. A nested pattern is expected when species assemblages in species-poor sites are a subset of those assemblages present in species-rich sites (fragment nestedness), or when ~~the presence of~~ 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 ~~contrast if~~ differential extinction (the likely cause of reduction of species across forest fragments) is caused by either a reduction in habitat availability, an increase in the distance between forest fragments as consequence of habitat deterioration, or if the nested pattern is associated ~~to~~ 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). Between years we visited (GB, DO and JDRF) each site from 8 to 20 times to compile a comprehensive bird list of each site. 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 the 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, seasonal and permanent streams (Hartshorn 1983). We obtained the area of each site, 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 the PV, and excluded the area on the Caribbean slope of RV because this area is covered with rain forest rather than by dry forest (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~~, because we considered that resident birds are more affected by local changes in land use and deforestation~~. Occasional ~~sights~~ of native species far from their normal geographic breeding distribution ranges were also excluded. ~~Therefore,~~ the dry-forest bird-community was composed ~~by~~ resident, breeding species with terrestrial habits. Each bird species was classified into one of three forest dependency categories ~~according to~~ Stiles (1985) with modifications ~~made~~ 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.

Statistical analyses

We used a Sørensen Similarity Index to evaluate similarity of bird species composition among sites and assessed the relationship between species composition and geographic distances between sites using a Mantel test. We also determined whether composition of resident species across dry forest fragments follows a nested distribution, or if each fragment 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 ~~evaluate~~ nestedness in the avifauna of dry forest fragments we ~~first constructed~~ presence/absence matrices in which rows and columns were fragments and species respectively, and then sorted rows (assemblages) and columns (species) by two criteria: along a gradient of fragments area, and along a gradient of rainfall seasonality. On these matrices we calculated the NODF metric (Almeida-Neto *et al*. 2008, Ulrich *et al*. 2009, Bairos-Moreira and Maltchik 2012) and used 999 permutations with the '*quasiswap*' algorithm to ~~validate~~ the model~~'s significance~~ (Miklós and Podani 2004) by determining if 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 ~~assesses independently~~ nestedness of species assemblages among sites (rows), and nestedness for occupancy or presence among species (columns), and for the entire matrix that we refer to as community (Almeida-Neto *et al*. 2008). NODF ~~assumes values from 0 to 100, and higher values indicate more nested assemblages~~.

We also inferred whether nestedness was either caused by differential extinction due to a reduction in area available habitat 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 departure from perfect nestedness. To obtain the significance of the D statistic we compared the calculated value (no. species that departure from perfect nestedness in the original matrix) with 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 matrices in which sites were first ordered by decreasing area and then along a gradient of seasonality (Fig. 1). Analyses were conducted for all species and for forest dependant species (categories 1 and 2 of forest dependence). These matrices test ~~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 ~~highest number of~~ resident species while CB and Dir had the ~~lowest number~~, but the number of species did not differ significantly across sites ($X^2 = 5.51$, df = 4, p = 0.2387; Table 1). RV had the lowest similarity in species composition when compared with other sites, whereas CB and Dir had highest similarity (Table 2). We did not find a correlation between geographic distance between sites and species richness (Mantel test = 0.42, p = 0.185; Table 2) r between area of fragments and species richness (r = 0.41, p = 0.494).

Area and rainfall seasonality affected similarly the nested pattern at three different levels: bird community (entire matrix), bird assemblages, and species occurrence among dry forest fragments. The community was significantly nested (based on ~~the~~ overlap and decreasing fill statistics- NODF) by area of dry forest fragments (NODF = 31.63, p = 0.001). Furthermore, species occupancy ~~showed a nested pattern~~ (N columns = 31.61, p = 0.001), but bird assemblages did not nest by area among sites (N rows = 65.61, p = 0.099). The dry forest avifauna also showed a eral nested pattern in the fragments ranked by a length of dry season gradient (NODF = 31.61, p = 0.001). Bird assemblages showed a nearly significant nested pattern in fragments ordered along this gradient of rainfall seasonality (N rows = 32.00, p = 0.061) and species occupancy was strongly nested along such gradient (N columns = 31.61, p = 0.001). The similarity of these results is ~~understandable since~~ sites ranked by area followed nearly the opposite order when sites are ranked along a seasonality gradient (Table 1).

The subset of forest dependent species (categories 1 and 2) were 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 (N rows = 42.15, p = 0.005), but not by area of fragments (N rows = 57.68, p = 0.397). The species occupancy nested along both gradients: seasonality (N columns = 24.13, p = 0.001) and area (N columns = 24.13, p = 0.001). ~~Lomolino's test did not detect effect of differential extinction due to reduction in habitat availability~~ (D = 120, R = 128.9, P = 0.336, %PN = 6.91 for all species; D = 80.0, R = 91.0, P = 0.19, %PN = 12.06), nor distance between fragments (D = 133, R = 128.7, P = 0.644, %PN = 3.32) on nestedness of bird assemblages in dry forest fragments. ~~We found similar results~~ when sites were ordered by a gradient of rainfall seasonality and for forest dependant species.

In general the proportion of species included in the three categories of forest dependency was similar for all sites (~~X~~^{2} = 7.66, df = 8, p = 0.4677; Fig. 2). RV (~~17.3~~%) and Dir (12.8%) had the ~~highest percentage~~ of forest dependant species (category 1), ~~whereas~~ SR (8.1%) and CB (9.6%) had the lowest percentages (Fig. 2). The number of forest dependant species (category 1) did not differ across sites (X^2 = 6.86, df = 4, p = 0.143; Fig. 2), but when the expected number of species is corrected by the area of each site (i.e., # spp/ha * total ha), the number of forest dependant species varied significantly across sites (X^2 = 111.35, df = 4, p<0.0000001; Fig. 3); SR had a lower number of forest dependant species than expected, and RV, Dir and CB a higher number of forest dependant species relative to its area.

DISCUSSION

Area frequently explains by itself a large percentage of the variance in number of species in archipelagos or isolated fragments (Herkert 1994, Kruess and Tscharntke 1994, Lida and Nakashizuka 1995, Barrantes *et al*. 2011). This pattern is the result of decreasing colonization and increasing extinction risk as the area of forest fragments or islands decreases (McArthur and Wilson 1967, Harris 1984). Environmental heterogeneity may also influence the number and/or composition of species in fragments. Fragments and islands with complex topography (e.g., altitudinal gradient, mountains) often have higher species richness, or at least a different subset of species when compared with islands or fragments with relatively homogeneous topographies (Primack 1998, Fernández-Juricic 2000, Mayr and Diamond 2001). The characteristics of the matrix around the fragments, connectivity between fragments, edge effect, and human intervention 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 the area of fragments. Sites with shorter dry season maintain a larger number of dry forest and forest dependant species. From a conservation perspective, forest dependent species are likely more susceptible to global climatic changes, particularly to changes expected 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 and viable 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.

The Lomolino analysis failed to identify distance and size of fragments as proximate causes of nestedness. 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 reduction (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., ~~*Calloceita*~~ *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, the 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 (e.g., distance among fragments).

Species composition across sites is apparently more related ~~with~~ vegetation features than with area of fragments or geographic isolation (e.g., distance). The area of the fragments included in this study does not predict the number of species present in each fragment. For instance, SR 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 PV are ~~covered~~ primarily ~~with~~ 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 forest fragments. 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 is necessary to preserve ecosystem diversity, e.g., through habitat restoration and fragment connection.

Our results indicate that between 8.4 to 17.9 % of all native species in dry forest fragments require large areas of mature forests and more than 50% of the species in each forest fragment require at least 50% of forest cover to maintain viable populations (Fig. 2; Stiles 1985). Hence, forest fragments 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 fragments 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 fragments 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 fragments 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 fragments 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 seriously threaten the long-term viability of many bird species. Nestedness analyses proved to be an important tool to evaluate the consequences of 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 avifauna (or other animals) in forest fragments.

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Table 1. Area, location and number of native species recorded in five dry forest fragments in northwestern Costa Rica. Length of dry season is indicated by ordinal categories, e.g., 1 indicates the shortest dry season

Locality	Abbreviation	Dry season	Area (ha)	Location	No. of species
Santa Rosa	SR	5	37117	10º50'N, 85º37'W	123
Palo Verde	PV	4	11970	10º20'N, 85º20'W	135
Rincón de la Vieja	RV	1	8411	10º49'N, 85º21'W	127
Diriá	Dir	3	5426	10º10'N, 85º35'W	109
Cabo Blanco	CB	2	1172	09º33`N, 85º06'W	104

Table 2. Values of the Sørensen similarity index between species composition (below the diagonal) and distance (km) (above the diagonal) between five forest fragments in northwestern Costa Rica. Fragment abbreviations as in Table 1.

		Distance				
		SR	PV	Dir	CB	RV
Similarity	SR		77.9	72.6	71.5	63.6
	PV	0.80		68.9	69.4	58.9
	Dir	0.82	0.71		70.6	61.3
	CB	0.81	0.67	0.85		64.6
	RV	0.73	0.62	0.70	0.76	

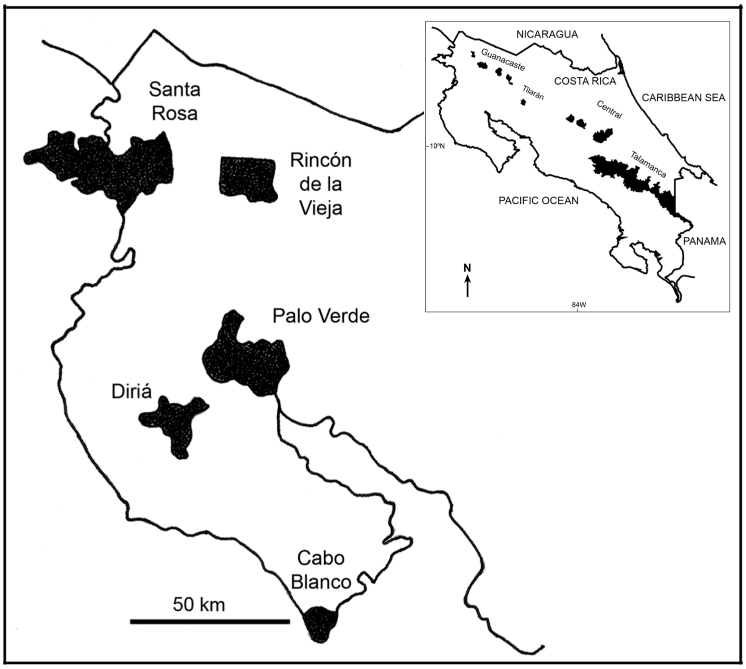

Fig.1. Dry forest fragments studied in northwestern Costa Rica. The inset shows the main cordilleras in Costa Rica.

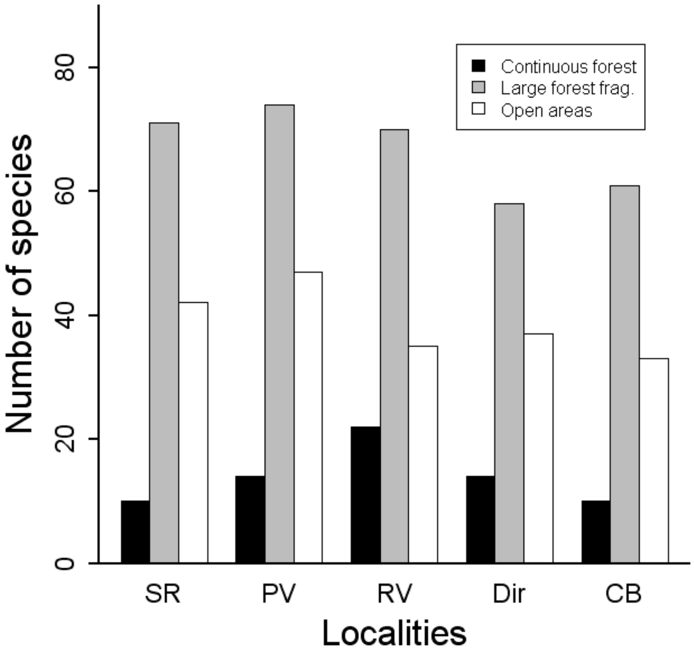

Fig. 2. Number of bird species included in the three categories of forest dependence for the five forest fragments in northwestern Costa Rica: SR - Santa Rosa, PV - Palo Verde, RV - Rincón de la Vieja, Dir - Diriá, CB - Cabo Blanco.

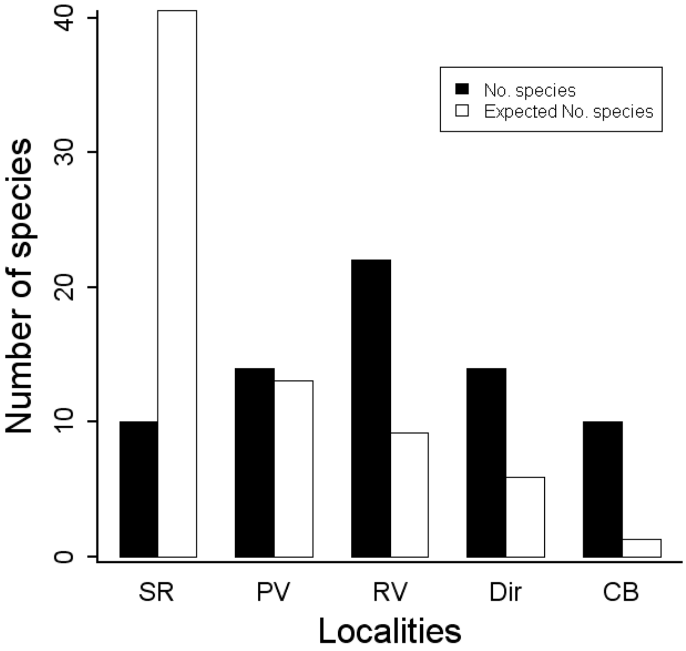

Fig. 3. Observed number of forest dependent species and the expected number corrected by area for five forest fragments in northwestern Costa Rica: SR - Santa Rosa, PV - Palo Verde, RV - Rincón de la Vieja, Dir - Diriá, CB - Cabo Blanco.