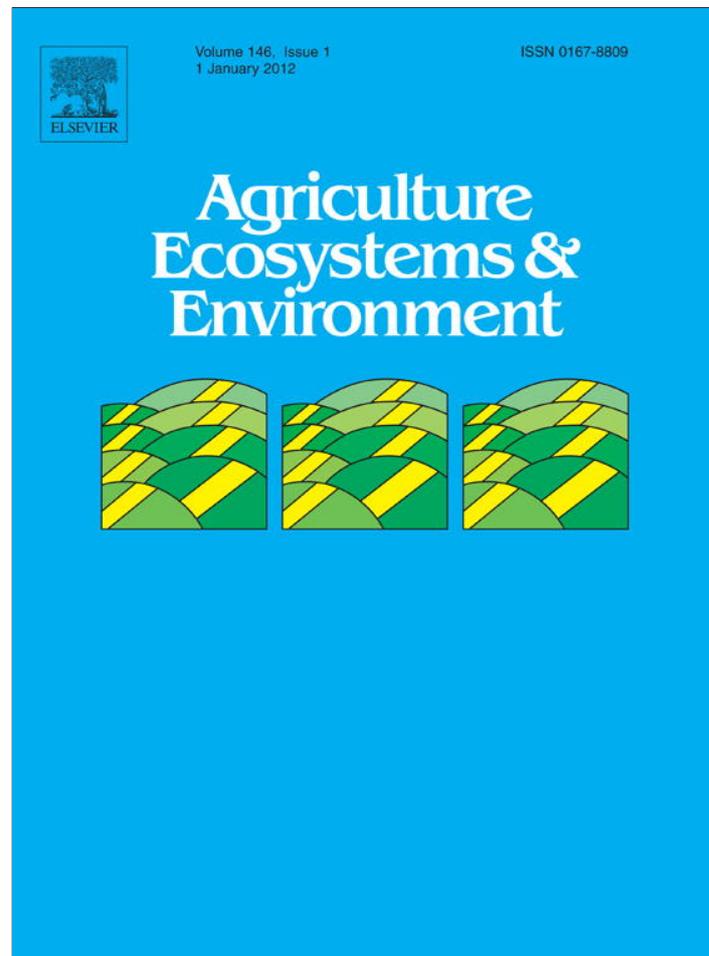


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Contribution of woody habitat islands to the conservation of birds and their potential ecosystem services in an extensive Colombian rangeland



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ABSTRACT

In agricultural landscapes, patches of natural or semi-natural habitat are crucial for the survival of plant and animal populations, which in turn are essential to maintain ecosystem functioning. Species composition and diversity of trees and birds among woody habitat islands were compared in a Colombian rangeland to assess how habitat characteristics influence bird community composition, bird species traits and their potential ecosystem services. Bird and tree diversity was higher in gallery forest fragments compared to hedgerows and isolated tree islands within rangelands. Forest fragments shared over 50% of their bird and tree species with tree islands and hedgerows, yet communities differed markedly. Tree islands and hedgerows had relatively more endozoochorous and small-seeded tree species and hosted birds of forest, savanna and shrubland, while forest fragments had more synzoochorous and large-seeded tree species and primarily hosted forest birds. Hedges and tree islands contribute to the conservation of forest bird and tree biodiversity in rangeland, but gallery forests are essential for the conservation of less tolerant forest species. The savanna rangeland acts as an ecological filter between the gallery forests and the hedges and tree islands, which in turn facilitate the spillover of tolerant forest birds and their ecological functions, including tree seed dispersal, into the rangeland, and thus support regional forest conservation and restoration.

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1. Introduction

Birds have important ecological functions which are essential for the provision of ecosystem services such as pollination, seed dispersal and pest control (Sekercioglu, 2006). In the tropics, habitat losses and habitat degradation, in particular in forests, are causing rapid declines in bird species, which in turn may cause reductions in ecosystem processes, services and benefits (Sekercioglu et al., 2004, 2012). In coffee agroforests, for example, reduced floristic diversity

leads to reduced control of insect populations by birds and thus to crop losses (Borkhataria et al., 2012; Philpott and Bichier, 2012). In disturbed forests, altered seed dispersal patterns, for instance due to declining populations of frugivores, may influence succession, cause regime shifts in plant communities and thus modify ecosystem functioning (Farwig and Berens, 2012; McConkey et al., 2012). The conservation of birds is, therefore, essential to maintain ecosystem services delivery across a wide range of habitats including human-dominated habitats such as farmland, agroforests and rangeland (Bradbury et al., 2010; García et al., 2010).

Conservation of forest birds and their services in tropical agricultural landscapes depends on the resilience of the bird communities to disturbance (Karp et al., 2011) and on the conservation of suitable habitats of varying quality in the farmland matrix (e.g. Sekercioglu et al., 2007; Aerts et al., 2008; Gavier-Pizarro et al., 2012; Martin et al., 2012). These habitats include forest fragments, isolated trees, tree islands and linear features such as hedgerows, riparian corridors and tree-lined roads (e.g. Fischer and Lindenmayer, 2002; Manning et al., 2006; Gillies and Clair, 2008; Lentini et al., 2011). The

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extent to which these habitats are suitable for forest birds depends on their structural complexity (Haslem and Bennett, 2008) and on the resources they have to offer, including food, nesting sites, and perches.

Here, the results of a tree and bird community study from the Llanos Orientales savanna rangeland in central Colombia are presented. The objectives of the study were to assess whether differences in plant communities among isolated woody habitats in the rangeland are reflected in bird communities and their potential ecosystem services. It was hypothesized that: (1) overall tree and bird species diversity is higher in remnant forests than in other woody habitat islands; (2) tree and bird species communities differ between forests and the other habitat islands; and (3) there are direct links between tree composition, habitat characteristics, bird species and bird species traits.

2. Methods

The study was conducted in the Llanos Orientales savanna near the municipality of Granada in the Meta department in central Colombia (360–380 m asl, 3°36' N, 73°43' W, Fig. A.1). The Llanos Orientales or Eastern Plains is a region of wide grassy plains with meandering rivers that flow from the Andean foothills in the west to the Orinoco River in the east. The study site is located 20 km east of the Andean foothills. The main soil types are orthic ferralsols (USDA: oxisols) and plinthic Acrisols (USDA: ultisols) with dystic fluvisols (USDA: fluvents) along the major rivers. Annual precipitation in the region averages 2500 mm, and drier seasons occur during January–February and July–August. The area is marked by a continuously hot climate, with a mean annual temperature of 24.8 °C and daily mean temperatures ranging between 24.0 and 25.6 °C. The natural vegetation is deciduous dry tropical forest, but most of the Llanos Orientales are covered with various types of anthropogenic savanna mainly used for cattle farming (Stevenson and Aldana, 2008). The grassy plains are interspersed with patches of natural vegetation, mainly tree islands and gallery forests along the meandering rivers. Grazing blocks are often lined with recent (<40 y old) hedgerows (Fig. A.2), consisting of trees or bushes naturally regenerating along the fences. Tree islands and hedgerows are highly appreciated by farmers as they provide services for the ranching system (e.g. to shade the cattle). The present study covered an area of approximately 400 ha which contained two continuous gallery forests with highly variable width (between 60 and 420 m wide), 200 tree islands, and 6 km of hedgerows that function as living fences (Fig. A.1). The gallery forests and the tree islands have had approximately the same area at least since 1970, while the living fences were established after 1982.

2.1. Study design

Between July and October 2011, vegetation composition and structure, abiotic site characteristics and birds were recorded in three habitat types representing forest and additional woody habitats in the savanna matrix, i.e. (1) gallery forest; (2) tree islands; and (3) hedgerows (Fig. A.2). Using a stratified random sampling design, 20 plots were placed in the two forests, 20 plots in 20 tree islands, and 10 plots along 5 hedgerows (Fig. A.1). The plots in forests and tree islands were circular, with a radius of 11.3 m, and those along hedgerows were rectangular (4 × 100 m), with the long side parallel to the hedgerow and the hedgerow running along the centerline of the plot. All plots were 400 m² in size, but some tree islands were smaller. For these small patches, effective patch size was estimated from two perpendicular patch diameter measurements.

2.2. Vegetation composition, structure and traits

To determine woody species composition and stand structure, height and diameter at breast height (dbh) were measured for all woody plants with a dbh > 5 cm, including standing dead trees. Stem density (stems/ha), basal area (m²/ha) (both corrected for effective patch size when necessary) and mean tree height (m) were calculated. Canopy cover (%) was calculated from 20 systematic measurements of canopy presence or absence using the Cajanus tube method (inner tube diameter: 0.5 cm). Grass cover (%) was calculated from Braun–Blanquet scores recorded in 10 1-m² subplots. In the same subplots, also the number of tree seedlings was counted. Average depth of the ectorganic horizon (mm) and soil depth (m) were calculated from five measurements at random locations within the plot. For soil depth the rod penetration method (rod diameter: 1 cm) was used. Dispersal mode (anemochorous, synzoochorous and endozoochorous) and seed size class (small: <0.5 cm width; medium: 0.5 ≤ width ≤ 1; large: width > 1) were assigned to all recorded species (following Stevenson and Aldana, 2008) and relative frequencies were calculated for all classes.

2.3. Bird surveys and traits

Point counts were used to determine bird species abundance and count stations were at the plot centres. All 50 point count locations were surveyed four times, with at least 20 days between counts at the same point. The order in which stations were counted was randomized, but successive counts were never performed in neighbouring stations. All point counts were conducted in relatively dry weather and between 0620 and 1100 h when birds were most active. At each point, all birds seen or heard up to a 30 m radius within a 10 min period were recorded, except flyover birds. For all recorded bird species, data on average body mass, minimum and maximum number of eggs laid, preferred habitat, habitat breadth (number of major habitat types used), tolerance to disturbance, primary diet and diet breadth (number of major food sources consumed) were obtained from a world bird ecology database with standardized entries on the ecology of all bird species of the world (Sekercioglu, 2012). For numerical traits, averages per plot were calculated for the species observed in that plot. For categorical variables, the proportions for all categories were calculated for every plot (=the number of occurrences of a category in a plot divided by the number of species in the plot).

2.4. Data analysis

For plant data, α (average species richness per plot), β ($=\gamma/\alpha$, total richness/average richness), γ (total richness per habitat type), and *Chao1* (expected species richness based on abundance data) were calculated. For birds α , β , γ and *Chao2* (expected species richness based on incidence-based data) were calculated. Mean species diversity (α) among habitat types was compared using Kruskal–Wallis one-way analysis of variance by ranks. *Chao1* and *Chao2* were calculated in EstimateS 8.2 (Colwell, 2009). Statistical tests, unless noted otherwise, were performed in IBM SPSS Statistics 20 (IBM Corp., New York, USA).

To compare community composition of birds and woody plants among the three different habitats, an indirect gradient analysis approach was adopted, with birds (presence data of species observed in at least two count stations) and woody plants (log₁₀ transformed basal area data of species present in at least two plots) analyzed separately. Multi-response permutation procedure tests (MRPP) were used to test for multivariate differences in community composition among habitat types. For MRPP, the Sørensen distance measure and a natural group weighting factor $n_i/\sum n_i$ were used, where n_i is the number of sample plots in each group.

Table 1
Woody plant and bird species diversity in gallery forests, tree islands and hedges in the Llanos Orientales savanna, Colombia.

	Forests (n = 20)	Tree islands (n = 20)	Hedges (n = 10)
Woody plants			
α (average plot diversity and SE)	22.2 (0.8)	18.4 (1.5)	16.7 (1.2)
β (turnover)	5.3	3.7	2.8
γ (total species richness)	117	69	46
Chao1 (expected species richness)	150	80	76
Birds			
α (average plot diversity and SE)	15.1 (1.3)	8.1 (1.1)	8.1 (1.8)
β (turnover)	3.8	5.0	3.5
γ (total species richness)	52	39	28
Chao2 (expected species richness)	68	52	42

The test statistic, T , describes the separation between groups while the chance-corrected within-group agreement, A , describes within-group homogeneity compared to random expectation (McCune and Grace, 2002). Indicator Species Analysis (Dufrene and Legendre, 1997) and Monte Carlo permutations (5000 runs) were used to calculate indicator values for all species and their significances within the three habitat types. Non-metric multidimensional scaling (NMS) was used to investigate indirect gradients influencing species distribution. NMS was run using the Sørensen distance measure, six starting dimensions, 500 iterations, an instability criterion of 10^{-7} and a rotation for maximum variance. NMS dimensions were related to plot and bird traits by use of the Spearman rank correlation coefficient (r_s). MRPP, indicator species analysis and ordination were performed using PC-ORD 5.31 (McCune and Mefford, 2006).

Non-parametric Kruskal–Wallis analysis of variance with Bonferroni correction for multiple comparisons was used to assess differences among forests, tree islands and hedgerows. To analyze overall multivariate similarities between different data sets, correlations between distance matrices were calculated, which is the method underlying techniques such as ANOSIM (Analysis of Similarity). Relative basal area data of plants, tree trait and environmental data, relative abundance data of birds and bird trait data were used to calculate four Sørensen distance matrices (plant species, plant-plot traits, bird species and bird traits). Mantel correlation coefficients and two-tailed significance values were then calculated for the six possible matrix combinations. Distance matrices and correlation coefficients were calculated with the package 'ecodist' in R 2.15.1. Finally, to interpret the overall patterns, the dataset was screened for bivariate correlations among bird and tree/plot traits using the Spearman rank correlation coefficient.

3. Results

A total of 133 woody plant species belonging to 50 families were recorded across all sites (Table A.1), of which 55 species only occurred in the gallery forests (41.4%). Forest sites had higher tree diversity (mean $\alpha = 22.2$ species) than tree islands (18.4 species) and hedgerows (16.7 species) (KW $\chi^2 = 17.8$, $p < 0.001$) (Table 1). Similar patterns were observed for tree species turnover, richness and expected richness (Table 1). Four species contributed to nearly one-third of the total recorded basal area: the tall forest tree *Pera arborea* accounted for 17.5%; the shrub *Erythroxylum* cf. *catartarum*, the understory palm *Attalea insignis*, and the evergreen shrub *Myrsine guianensis* each accounted for 5%.

A total of 1007 individual birds belonging to 66 species were recorded across all sites (Table A.2) and belonged to 33 families and 21 feeding guilds. All birds belonged to the Neotropical realm, except three species that are also found in the Nearctic realm. No restricted-range or threatened species were observed. Total and expected species richness values were higher in forests than in tree islands and hedgerows (Table 1). From the total species pool, 52

bird species (72.2%) occurred in forest, of which 21 (29.2%) were restricted to forests and 31 (43.1%) also occurred outside forests. Forest shared more species exclusively with tree islands (9 species; 12.5%) than with hedgerows (4 species; 5.6%) (Table A.2). Forest sites had a higher bird alpha diversity than tree islands and hedgerows (KW $\chi^2 = 15.1$, $p = 0.001$) (Table 1). Bird species turnover was higher in tree islands (Table 1). Four species accounted for one-third of all birds recorded: the forest bird *Cyanocorax violaceus* was the most abundant (16.7% of all records) followed by *Crotophaga ani* (7%; a bird of shrublands), *Tyrannus melancholicus* (5%; a bird of savannas), and *Ramphocelus carbo* (5%; a bird of forests) (Fig. A.3).

3.1. Plant and bird communities

Plant and bird communities were highly distinct among forest, tree island and hedgerow habitats ($p < 0.001$ for both trees and birds). Homogeneity within habitats ($A_{trees} = 0.077$; $A_{birds} = 0.062$) and separation between habitats ($T_{trees} = -13.52$; $T_{birds} = -8.92$) was more pronounced for woody plants than for birds. A wide variety of woody indicator species was significantly associated with forests, *Siparuna guianensis* and the palm *A. insignis* being most indicative of this habitat type (Table 2). Tree islands and hedgerows had fewer indicators. A *Vismia* species and the fruit tree *Byrsonima crassifolia* were most indicative for hedgerows while two other fruit trees, *Rollinia edulis* and the palm *Acrocomia aculeata*, were significant indicators for tree islands (Table 2). A similar pattern emerged for birds: forests had a wide variety of significant bird indicator species, while hedgerows had only two and tree islands none. *Arremon taciturnus*, *Ramphocelus carbo*, *Tolmomyias flaviventris*, *Buteo magnirostris* and *Manacus manacus* were the strongest indicators for forest – these species and the other indicator species of the forest plots are birds of forest and woodland (Table 2). The indicators for hedgerows were *Zenaida auriculata* and *Mimus gilvus*, birds of shrubland and savanna, respectively (Table 2).

3.2. Plant and bird traits

Plant and bird traits varied markedly among habitats, with the main contrasts mostly occurring between forest and other woody habitat in the matrix. Forests had, on average, taller trees, higher canopy cover, more seedlings and lower grass cover than tree islands and hedgerows. Tree islands and hedgerows had relatively more endozoochorous and small-seeded, species (Fig. 1a and b). Synzoochorous and large-seeded tree species were restricted to forests (Fig. 1a and b). The proportion of forest specialists was lower and those of savanna and shrubland species higher outside forests (Fig. 1c). General dietary differences did not emerge, except for a slightly higher relative abundance of seed-eaters and lower abundance of birds preying on vertebrates outside forests (Fig. 1d). The differences among habitats were stronger for plants than for birds, because only those observed for plants were significant after Bonferroni correction for multiple comparison (Table A.3).

Table 2
Woody plant and bird indicator species of gallery forests, tree islands and hedgerows in the Llanos Orientales savanna, Colombia.

Woody species			Birds		
Species	IV	<i>p</i>	Species	IV	<i>p</i>
Forests					
<i>Siparuna guianensis</i>	64	<0.001	<i>Arremon taciturnus</i>	50	<0.001
<i>Attalea insignis</i>	60	<0.001	Pectoral sparrow (F)		
<i>Bellucia grossularioides</i>	53	<0.001	<i>Ramphocelus carbo</i>	50	0.002
<i>Garcinia macrophylla</i>	50	<0.001	Silver-beaked tanager (F)		
<i>Forsteronia cf. affinis</i>	40	0.002	<i>Tolmomyas flaviventris</i>	45	0.001
<i>Phenakospermum guyanense</i>	40	0.002	Yellow-breasted flycatcher (W)		
<i>Alchornea triplinervia</i>	40	0.005	<i>Buteo magnirostris</i>	45	0.003
<i>Lacistema aggregatum</i>	39	0.003	Roadside hawk (F)		
<i>Protium sagotianum</i>	35	0.005	<i>Manacus manacus</i>	43	0.003
<i>Pseudolmedia laevis</i>	35	0.007	White-bearded manakin (W)		
<i>Euterpe precatória</i>	35	0.010	<i>Galbula tombacea</i>	35	0.004
<i>Inga cf. alba</i>	35	0.007	White-chinned jacamar (F)		
<i>Lacmellea gracilis</i>	25	0.032	<i>Sakesphorus canadensis</i>	35	0.004
<i>Inga acreana</i>	25	0.033	Black-crested antshrike (W)		
Tree islands					
<i>Rollinia edulis</i>	44	0.007	<i>Pitangus sulphuratus</i>	29	0.035
<i>Acrocomia aculeata</i>	25	0.018	Great kiskadee (W)		
Hedgerows					
<i>Vismia sp. 1</i>	65	<0.001	<i>Mesembrinibis cayennensis</i>	27	0.018
<i>Byrsonima crassifolia</i>	54	<0.001	Green ibis (F)		
<i>Erythroxylum cf. cataractarum</i>	54	0.003	<i>Crypturellus cinereus</i>	25	0.018
<i>Myrsine guianensis</i>	51	0.002	Cinereous tinamou (F)		
<i>Vismia cayennensis</i>	33	0.016	<i>Thryothorus leucotis</i>	25	0.018
			Buff-breasted wren (W)		
			<i>Trogon viridis</i>	25	0.019
			White-tailed trogon (F)		

IV, indicator value, ranges from 0 (no indication) to 100 (perfect indication).

P, proportion of 1000 randomized trials with IV equal to or exceeding the observed IV. Only species with *P* < 0.05 are listed.

For birds, preferred habitats are indicated as (F) forest, (W) woodland, (SH) shrubland, and (SAV) savanna.

The NMS ordinations unmistakably separated forest habitat from non-forest habitat both for woody species (Fig. 2a) and birds (Fig. 2b), with some overlap between forest plots and larger tree islands in the plant ordination (Fig. 2a). For the plant data, the main gradient represented increasing grass cover and decreasing canopy cover, seedling density and litter depth; for the bird data, the main gradient represented a decreasing preference for forest habitat (rank correlations and significance: Table A.4).

Bird and tree species and traits exhibited strikingly similar overall patterns. Differences in bird traits followed differences in bird species composition and differences in tree and plot traits followed differences in tree relative dominance. More interestingly, differences in bird relative abundances also followed differences in tree relative dominance and tree/plot traits; and differences in bird traits also followed differences in tree/plot traits (Table 3). These broad patterns were reflected in some interesting direct correlations between the relative frequencies of preferred habitats of birds and the tree and plot traits. There was a direct positive relation between the relative frequency of forest birds and the seedling density ($r_s = 0.306$; $p = 0.030$), the relative frequency of synzoochorous species ($r_s = 0.323$; $p = 0.002$) and large-seeded tree species ($r_s = 0.323$; $p = 0.002$); the relative frequency of savanna birds was positively correlated with the relative frequency of endozoochorous species ($r_s = 0.337$; $p = 0.017$) and negatively with canopy cover ($r_s = -0.335$; $p = 0.017$) and tree height ($r_s = -0.397$;

$p = 0.004$); and the relative frequency of birds that feed on invertebrates was positively correlated with the basal area of dead trees ($r_s = 0.383$; $p = 0.006$).

4. Discussion

The results supported the hypotheses that tree and bird diversity is higher in forests than in tree islands or hedgerows (Table 1), and that communities of trees and birds differ significantly among those habitats (MRPP test), principally between forest and other woody habitat in the savanna matrix (NMS ordination, Fig. 2). Tree and bird species and traits among habitats exhibited similar patterns (Table 3), but only a limited number of direct relations between different traits were found. Higher diversity and abundance of birds and trees in forests was expected because forests were the least-disturbed and more natural habitats, while the tree islands and hedgerows were, essentially, components of an anthropogenic and heavily disturbed matrix, which is usually less suitable for the conservation of forest biodiversity (e.g. Mahood et al., 2012; but see Haslem and Bennett, 2008). Nevertheless, both for trees and birds higher diversity and abundance in forests may also be related to passive sampling, i.e. the increase of species richness and abundance with area. The extent of gallery forests in the region is larger than the area of tree islands and hedgerows, and forests can therefore support more species (see e.g. Burns et al., 2010). In

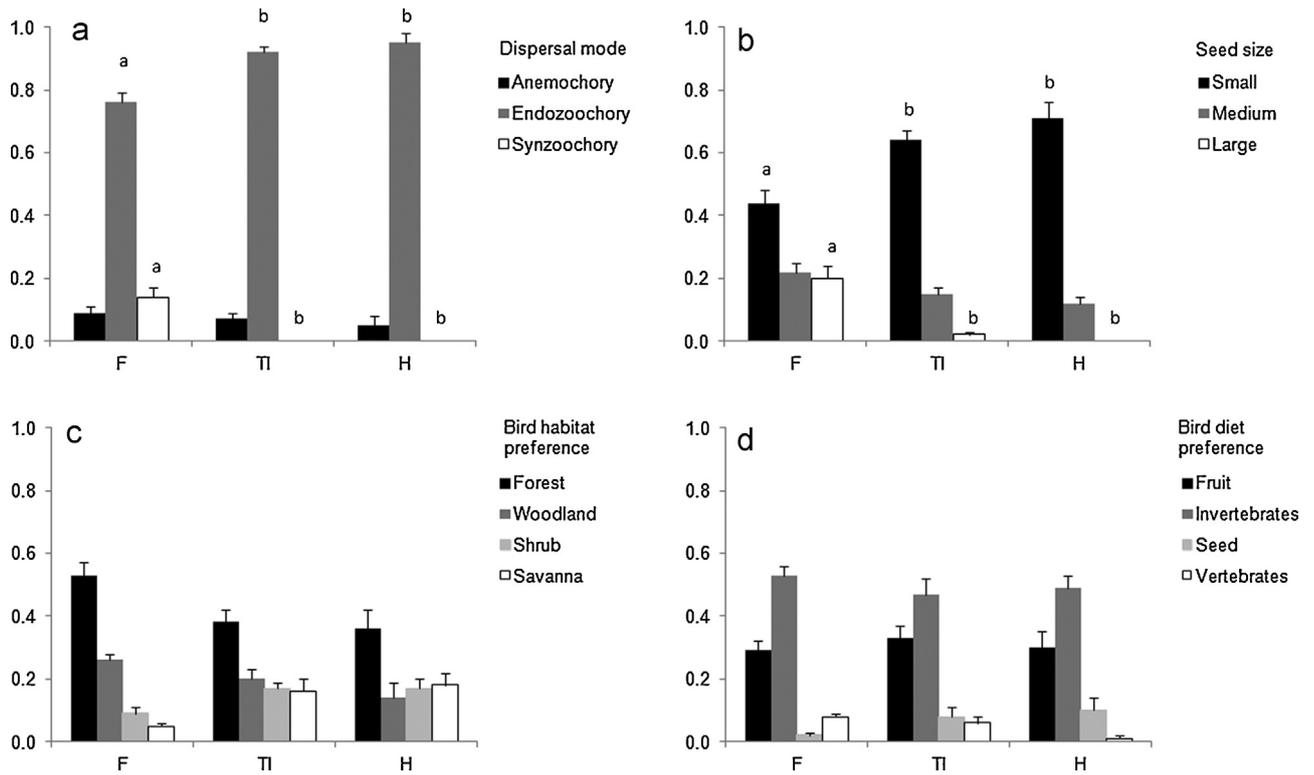


Fig. 1. Patterns in the mean relative frequencies (error bars denote SE) of (A) dispersal modes and (B) seed sizes of trees, and (C) habitat preferences and (D) diets of birds in forests (F), tree islands (TI) and hedges (H) in the Llanos Orientales, Colombia. Letters show pairwise differences between habitat types according to non-parametric Kruskal–Wallis ANOVA by ranks and Bonferroni-corrected significance level 0.0017 (Table A.3).

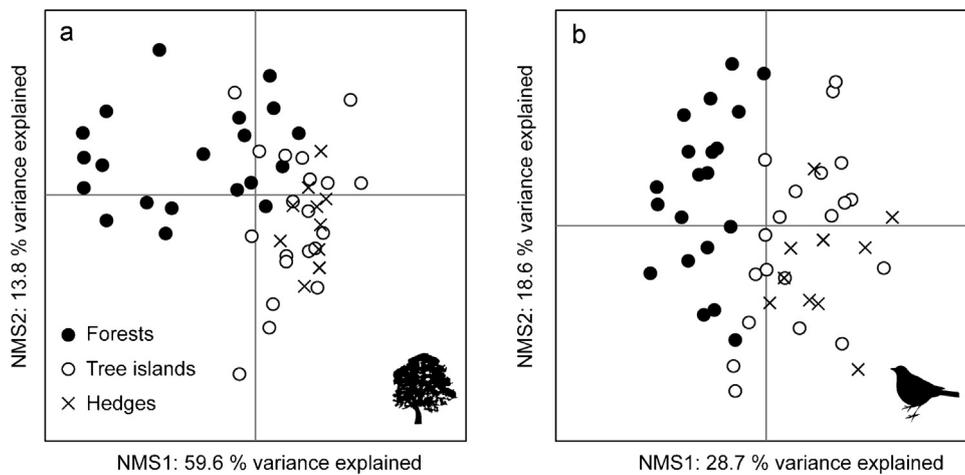


Fig. 2. Non-metric multidimensional scaling (NMS) analysis of differences in community composition of (A) woody plants and (B) birds, among forest, tree islands and hedges in the Llanos Orientales, Colombia.

Table 3

Multivariate similarities among bird and tree species and traits in forests, tree islands and hedges in the Llanos Orientales savanna, Colombia, based on Mantel tests between pairs of Sørensen distance matrices (Mantel *r* above diagonal; significance *p* below).

		Trees		Birds	
		Relative dominance	Traits	Relative abundance	Traits
Trees	Relative dominance	–	0.360	0.187	0.058
	Traits	0.001	–	0.257	0.176
Birds	Relative abundance	0.002	0.001	–	0.339
	Traits	0.393	0.001	0.001	–

a comparable study in the Colombian Andes, live fences also supported diverse plant and bird communities which were subsamples of the original forest species pools (Pulido-Santacruz and Renjifo, 2011). The differentiation among communities was stronger for plants than for birds, because birds are, by nature, more mobile than plants, but also because some tree species are clearly affected by dispersal limitation.

When comparing forests and agricultural areas with respect to the diets of tropical bird species, the species richness of large frugivores and insectivores usually declines with increasing simplification of habitat (Sekercioglu, 2012). The study area may have already lost such forest specialists because of the rather fragmented nature of the riverine forest system and the virtual absence of forest core area due to edge effects related to the narrow width of the forests. Yet a similar decline in the numbers of bird species preferring fruit or invertebrates was found when comparing forests to tree islands and hedgerows (42 species in forests; 33 in tree islands; 23 in hedgerows). This decline was essentially caused by an overall decline of species richness over the forest-tree island-hedgerow gradient (Table 1), as the relative frequencies of frugivores and insectivores did not differ significantly among habitat types (Fig. 1d). The conservation of guild proportionality across habitats in avian communities implies that, potentially, the variety of ecosystem services such as seed dispersal by frugivores or pest control by insectivores is also conserved. The decrease in species richness, however, means that less species are available to deliver those services. Even when the total number of individual birds remains stable, there is a decrease in ecological redundancy. In the biodiversity–ecosystem functioning perspective (Loreau et al., 2001), lower redundancy is related to lower ecosystem resilience and stability (Laliberte et al., 2010), with negative impacts on ecosystem functioning in the longer term (Reich et al., 2012). In species-poor communities, the loss of one or a few species may have a much larger impact on ecosystem services than in species-rich communities. Recent evidence from temperate secondary forest shows that seed dispersal quantity (number of seeds and seed species being dispersed) and, more importantly, quality (the fine-scale pattern of seed dispersal) are principally determined by frugivore assemblage richness (García and Martínez, 2012). Arthropod removal rates in tropical agroforests were also best predicted by bird species richness (Philpott et al., 2009). High diversity seems to be indispensable to maintain ecosystem services (Isbell et al., 2011). Avian ecological function in tree islands and hedgerows is likely to be less effective and more sensitive to environmental changes.

When considering the dispersal modes and seed sizes of trees in the different habitats (Fig. 1a and b), the absence of large-seeded and synzoochorous tree species in the tree islands and hedgerows is apparent. While differential effects of grazing on tree seedlings cannot be ruled out, this may be related to the earlier postulation that large frugivores, such as macaws and curassows, have already disappeared from the studied landscape because of the lack of suitable forest core habitat, or to the filtering effect of the open matrix that will only be crossed by tolerant species that feed on small seeds. Nevertheless, seedlings emerged in both tree islands and hedgerows in the order of one seedling per 1–2 m² (Table A.3). Both habitats could, therefore, play important roles in the restoration of forest at the landscape scale, especially when cattle is excluded temporarily (Aerts et al., 2009). Isolated tree islands can act as nuclei for forest regeneration (Corbin and Holl, 2012), even at large distances from forests (Lasky and Keitt, 2012). Hedgerows may have an important corridor function. Extending the network of hedgerows would increase the connectivity between forest fragments by increasing the tree cover at landscape scale and thus reducing the average distance between tree canopies (Harvey et al., 2005; Manning et al., 2006). Hedgerows may also increase the

permeability of the landscape for bird species that are less tolerant of open grasslands (Davies and Pullin, 2007; Gillies and Clair, 2008; Vergara, 2011), hereby facilitating plant–bird interactions such as pollination and seed dispersal (Tewksbury et al., 2002). The positive effects of increased structural complexity in the landscape may also extend to other taxa, including fruit-eating bats, hereby reducing the current filtering effect of the savanna and thus enhancing seed dispersal from forests (Muscarella and Fleming, 2007; but see Gonzales et al., 2009). The absence of large-bodied avian frugivores nevertheless means that regenerating forest is expected to be biased towards small-seeded zoochorous tree species, as already observed in tree islands and hedgerows (Fig. 1b) and in logged tropical forests elsewhere (Velho et al., 2012).

Nearly 30% of the total bird species pool was restricted to forest habitat, and these included species with a wide range of diets and feeding strata, such as *Crypturellus cinereus*, *Galbula tombacea*, and *Trogon viridis*. The gallery forests in the Llanos Orientales are, therefore, not only vital for the survival of forest trees but also for the conservation of forest birds, even when the high habitat breadth and tolerance to disturbance of the birds recorded in the forests indicate that the forest is disturbed (Table A.3). Studies in farmland habitats elsewhere, including silvopastoral systems in the Argentine Chaco (Mastrangelo and Gavin, 2012) and cattle-coffee producing countryside in Costa Rica (Hughes et al., 2002), also demonstrated the importance of forest for bird conservation. Even more so, as conservation of the remaining forest fragments and their biodiversity, functions and services is unlikely to be sufficient to meet the increasing demands for ecosystem services provided by forests (for instance, climate regulation; Aerts and Honnay, 2011), passive or active forest restoration may be required in the long term (Lamb et al., 2005; Holl and Aide, 2011). As highlighted above, the isolated tree islands and hedgerows may be instrumental to achieve forest restoration at the landscape scale by facilitating the spillover of more tolerant forest birds and their ecological functions, including tree seed dispersal, from forest to smaller woody elements in the savanna. But if choices have to be made then priority should be given to the expansion of current high-quality forest fragments, for instance where the gallery forests are extremely narrow, to take optimal advantage of the species–area relationship in fragmented habitats (Huth and Possingham, 2011).

Data archiving statement

Data for this study are available at PANGAEA. doi: 10.1594/PANGAEA.788547.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2013.04.006>.

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