Journal of Biogeography (*J. Biogeogr.*) (2007)

ORIGINAL ARTICLE

Environmental correlates of avian diversity in lowland Panama rain forests

Ghislain Rompré[1]*, W. Douglas Robinson[2], André Desrochers[1] and George Angehr[3]

[1]Centre d'étude de la forêt, Faculté de foresterie et de géomatique, Université Laval, Québec, QC G1K 7P4, Canada, [2]Oak Creek Lab of Biology, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA and [3]Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-00948, USA

ABSTRACT

Aim The composition of communities is known to be influenced by biogeographical history, but also by local environmental conditions. Yet few studies have evaluated the relative importance of the direct and indirect effects of multiple factors on species diversity in rich Neotropical forests. Our study aims to assess drivers of change in local bird species richness in lowland tropical rain forests.

Location Thirty-two physiographic subregions along the corridor of the Panama Canal, Panama.

Methods We mapped the distributions of all forest-dwelling bird species and quantified the environmental characteristics of all subregions, including mean annual rainfall, topographic complexity, elevational variability, forest age and forest area. Plant species richness, believed to be correlated with structural complexity, was estimated by interpolation through kriging for subregions where data were unavailable.

Results The study region has a strong rainfall gradient across a short distance (65 km), which is also accompanied by steep gradients in plant and bird species diversity. Path analysis showed that precipitation strongly affected plant species diversity, which in turn affected avian diversity. Forest age and topography affected bird diversity independently of plant diversity. Forest area and its proportion occurring in the largest two fragments of each subregion (habitat configuration) were also positive correlates of bird species richness.

Main conclusions Our results suggest that plant species richness, known to be influenced in part by biogeographical history and geology, also affects bird species assemblages locally. We provide support for the hypothesis that bird species richness increases with structural complexity of the habitat. Our analysis of the distributions of the region's most disturbance-sensitive bird species showed that subregions with more rainfall, more complex topography and older forests harboured not only richer communities but also more sensitive species; while subregions with the opposite characteristics usually lacked large fractions of the regional forest bird community and hosted only common, widely distributed species. Results also emphasize the importance of preserving forest diversity from habitat loss and fragmentation, and confirm that larger, continuous forest tracts are necessary to maintain the rich avian diversity in the region.

Keywords

Avian diversity, biogeographical history, distribution patterns, environmental correlates, habitat heterogeneity, Neotropical rain forest, Panama Canal corridor, path analysis, plant species richness, species sensitivity.

*Correspondence: G. Rompré, Centre d'étude de la forêt, Faculté de foresterie et de géomatique, Université Laval, Québec, QC G1K 7P4, Canada.
E-mail: ghislain.rompre.1@ulaval.ca

www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2006.01657.x

INTRODUCTION

Patterns in the distribution of species diversity are the result of ecological, physical and historical factors across time and space (Vuilleumier & Simberloff, 1980; Currie & Paquin, 1987; Kerr & Packer, 1997; Hill & Hill, 2001; Hurlbert & Haskell, 2003; Hawkins *et al.*, 2005, 2006). Whereas biogeographical history influences the characteristics of species assemblages and therefore puts bounds on the composition of local communities (Ricklefs, 2004), local community composition is also strongly affected by local environmental (abiotic and biotic) conditions (Ricklefs, 1987; Wiens & Donoghue, 2004). In humid equatorial forests, for example, where relatively stable environmental conditions occur all year round, small differences in climatic or physical conditions can have important effects on species diversity (Fjeldså *et al.*, 1999; Kessler *et al.*, 2001). Specific examples include the increase in plant and bird diversity with variation in mean annual rainfall (Gentry, 1982; Cueto & Lopez de Casenave, 1999; Gillespie & Walter, 2001; Hawkins *et al.*, 2005; Schnitzer, 2005), topographic complexity and variability of elevation (Kerr & Packer, 1997; Kerr *et al.*, 2001; Rahbek & Graves, 2001). Many potential explanations for diversity gradients have been proposed, including species–energy relationships (Hurlbert & Haskell, 2003; Hurlbert, 2004), habitat heterogeneity–animal species diversity relationships (Kerr & Packer, 1997; Tews *et al.*, 2004) and historical factors (Ricklefs & Schluter, 1993; Ricklefs, 2004; Hawkins *et al.*, 2006). Few studies have examined relationships across small geographical areas in the species-rich tropics.

Despite the recognition that multiple environmental factors influence patterns of species distributions in tropical settings, few extensive biogeographical data sets are available for evaluating the relative importance of multiple factors, especially in Neotropical rain forests (Ricklefs & Schluter, 1993; Clark *et al.*, 2001; Currie *et al.*, 2004). Southern Central America provides an ideal opportunity for assessing drivers of change in local species richness (Condit *et al.*, 2002). This is especially true in lowland tropical forests in central Panama, near the Panama Canal, where steep gradients in species diversity occur in conjunction with high geographical variability in annual rainfall, underlying geology, topography and elevation across a very small area. Condit (1998), Pyke *et al.* (2001) and Schnitzer (2005) showed how plant species richness varies from the drier Pacific coast to the wetter, evergreen forests on the Caribbean coast. Condit *et al.* (2001) and Robinson *et al.* (2004) documented broad-scale distribution patterns of forest bird richness, revealing the lowest species richness (12 species) near the Pacific coast and more than 170 species in Caribbean coastal forests. In the latter studies, only forest area and rainfall were evaluated as possible drivers of bird species richness patterns, although other factors could also be involved.

Factors such as the composition of plant communities and forest type, which are influenced by site history and other environmental factors (Pyke *et al.*, 2001), have recently been studied in association with patterns of species richness of forest-dwelling birds (Gillespie & Walter, 2001; Kessler *et al.*, 2001; Waltert *et al.*, 2005). Habitat structural complexity, according to the habitat heterogeneity hypothesis, might explain the diversity gradients of birds (Tews *et al.*, 2004). A basic approach to understanding diversity patterns is to use multiple regressions. However, multiple regressions do not allow a comparison of different causal frameworks with the same set of environmental variables. Few tropical studies have used multiple regressions to study avian diversity patterns, and to our knowledge, none have compared possible causal frameworks linking hypothesized factors and identified statistically the relative importance for each of them.

In this study, we present a detailed analysis of fine-scale bird distribution patterns across a small region of central Panama, in 32 geographical regions with a high variability in abiotic and biotic conditions as well as a steep gradient in bird diversity. We conducted exhaustive field inventories to describe the distribution of species richness of forest-dwelling birds and to associate those spatial distribution patterns with components of the local environment using structural equation modelling (path analysis) to evaluate the relative strength and structural link between climate, topography, plant and bird diversity. Finally, we applied our understanding of key environmental correlates to identify areas in which bird species sensitive to habitat disturbance occur most often, therefore allowing opportunities to apply these data to conservation of the regional avifauna.

METHODS

Study area

General description

We studied lowland rain forests in central Panama along the Panama Canal corridor, an area of 65 km × 45 km (Fig. 1).

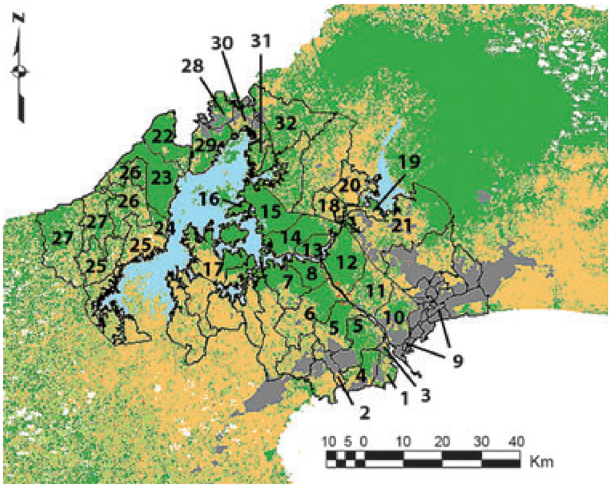

Figure 1 Physiographic subregions in the canal corridor, central part of Panama. Black lines and numbers indicate all the regions used for the study. Dark green, forests; light green, shrubs; yellow, pastures; grey, urban; and red, bare soil. Water from the canal is indicated in light blue. Digitized map from 1999 provided with kind permission by the ACP (Panama Canal Authority).

The region experiences a strong rainfall gradient: mean annual precipitation rises from 1500 mm year^{-1} on the Pacific coast to > 4000 mm year^{-1} in some regions on the Caribbean coast (Windsor *et al.*, 1990). Altitude varies from sea level on the coasts to 60 m a.s.l. along the canal, to 300–500 m a.s.l. in the foothills east and west of the canal. Most of the forest has been disturbed by humans in the last few centuries, especially on the Pacific slope near Panama City, but some old-growth patches remain on the Caribbean slope. Most of the region's forests are considered to be mature secondary stands (ANAM, 2003). Almost 50% of the current forest cover of the area is contained in national parks and other protected areas. The remainder of the forest is not formally protected, and mostly consists of a mosaic of fragments interspersed with regenerating second-growth, pastures and urban areas. Human impacts have been strong in the canal corridor, especially where urban influences are concentrated around two major cities (Panama City, the capital, and Colon). Yet Panama is unique among Latin American landscapes in that it still has a high percentage of forest cover close to its major cities. Within the different regions in this study, loss of forest cover through conversion to urban and agricultural land uses varies from less than 10% to more than 98% of their area (see Fig. 1). Up to 533 terrestrial bird species have been recently recorded in the region, from a total of 972 species for the whole country (Angehr, 2006). Angehr (2003), using criteria developed by BirdLife International, identified seven globally important bird areas, within the study area, based on the presence of restricted-range and globally threatened species.

Selection of subregions

We divided the canal corridor into physiographic subregions based primarily on boundaries of politically administered counties (*corregimientos*). Some counties were much larger than others and contained greater physiographic complexity. To reduce the variability within each of our subregions, we divided some of the larger *corregimientos* into smaller subregions based on obvious differences in underlying geology, topographic complexity or elevational range. This resulted in 32 subregions that formed the basis of our bird inventories. Boundaries of the 32 physiographic subregions were obtained (or created when *corregimientos* were divided by us) from digitized data from the Contraloria Nacional de Panama, with ArcGIS (ESRI, 2001). Here, we report results from inventories with subregions as sampling units. To simplify the analysis and presentation we have not presented data from each forest fragment that was sampled, even though most subregions had more than one forest patch.

Environmental characteristics of subregions

Each region was characterized by a combination of environmental factors potentially important to bird distribution patterns (Table 1). Correlates of distribution patterns of bird species richness were examined using environmental variables known to be associated with species richness in the tropics (Gentry, 1982; Clinebell *et al.*, 1995; Rosenzweig, 1995; Rahbek & Graves, 2001; Hurlbert & Haskell, 2003; Hawkins *et al.*, 2005; Pautasso & Gaston, 2005). We did not consider temperature in our analyses because it varies little across the subregions; temperatures range daily and annually from 22 to 30°C throughout our study site; which is typical of lowland tropical rain forests (Garwood, 1983).

Precipitation

Mean annual precipitation data were obtained from the Panama Canal Authority (ACP) and atlases (see also Condit, 1998; Pyke *et al.*, 2001; Santiago & Mulkey, 2005). The ACP has data extending back more than 100 years, but we used data from 1994 to 2003 to calculate mean rainfall per year for each subregion. That decade was characterized by 2 years with significantly below normal rainfall, 1 year with significantly above normal rainfall, and an overall average that was similar to averages from the previous four decades (Windsor *et al.*, 1990; Condit, 1998). For the remaining subregions which do not have rain gauges, we interpolated precipitation data from isohyets available from atlases of that period. We then compared these data with recent works by Condit (1998), Pyke *et al.* (2001) and Santiago & Mulkey (2005) to verify the accuracy of our data.

Topography

We used digital elevation data (resolution of 3 arcsec or 90 m, STRM-90; http://www.mapmart.com/DEM/countries/Panama.htm) and topographic maps to estimate topographical

Table 1 List of the environmental (abiotic and biotic) variables used to compare the 32 subregions of the Panama Canal corridor

Environmental variables	Sources
Plant species richness	Pyke *et al.* (2001), Pérez *et al.* (2005)
Mean annual precipitation (mm)	ACP, Panama; Pyke *et al.* (2001), Santiago & Mulkey (2005)
Elevation variability (maximum minus minimum elevation recorded, m)	Topographic maps
Topographical complexity (class of 1, flat, to 5, high complexity)	Digital elevation data, topographic maps (see text)
Age (1 = secondary forest, 2 = mature secondary, 3 = primary mature forest)	ANAM, Pyke *et al.* (2001)
Forest area (expressed by km^2 of forest area within each region)	Digitized maps (ACP, Panama)
Degree of fragmentation (% forest area included in one or two fragments)	Digitized maps (ACP, Panama)

variation within each subregion. Subregions were classified on a categorical basis on a scale of 1 to 5 (1 being relatively flat, with little variability in elevation and few dissected basins, 5 having high variability in elevation, and many ridges, ravines or steep slopes). This was done by calculating the proportion of slopes in each subregion, each being one to five times the steepness of the slope from the preceding category.

Elevational variability

Variability in elevation (in m) was determined by calculating the maximum altitude (a.s.l.) in each subregion minus minimum altitude (a.s.l.), which was frequently the altitude of the canal waters. This was done using topographic maps and digital elevation data. In the subregions of the canal corridor, elevational variability does not exceed 500 m. This measure is considered a reliable estimate of landscape heterogeneity (Kerr & Packer, 1997; Rahbek & Graves, 2001).

Tree species richness

We used data on plant species richness as a possible correlate of bird diversity because more species-rich forests tend to have greater foliage height diversity and the latter is recognized to be positively correlated with avian species richness (MacArthur *et al.*, 1962; MacArthur, 1964). In the Panama Canal region, vegetation richness is thought to be associated with the structural diversity of the habitat (Condit, 1998; Pyke *et al.*, 2001; DeWalt *et al.*, 2003). Floristic data were taken from inventories by Condit (1998), Pyke *et al.* (2001) and Pérez *et al.* (2005). For each of the inventories, all trees ≥ 10 cm d.b.h. were identified to species (full details of the method can be found in Pyke *et al.*, 2001). Since data were collected in 55 plots across the watershed of the canal and nested within 11 of the 32 subregions, we generated an interpolated geographical surface of plant richness by kriging (Rossi *et al.*, 1992; Maurer, 1994; see also Diniz-Filho *et al.*, 2002). This procedure provided robust data without the use of interpolated regression (see Rossi *et al.*, 1992). Since floristic data are difficult to obtain due to the high complexity of plant communities in the regions, and since detailed surveys are currently under way by researchers from the Smithsonian Tropical Research Institute in Panama (Pyke *et al.*, 2001; Pérez *et al.*, 2005; R. Condit, personal communication), the kriging method gave us a powerful tool with which we could compare bird species richness. The geostatistical procedures were performed using ARCMAP® software (Environmental Systems Research Institute, USA). By using the centroid of each subregion, we were able to calculate a plant richness value for each of them (Table 2).

Forest age class

Forest age was determined for each subregion by an age classification scheme that was already available (Pyke *et al.*, 2001; ANAM, 2003). Categories included: (1) secondary forest, (2) mature secondary, and (3) old-growth or primary forest. Age class was estimated using ANAM (2003) criteria, based on species composition and history of forest disturbance. Secondary forests are those disturbed in relatively recent history (< 100 years ago), mature secondary forests are those last disturbed more than 100 years ago, while old-growth forests are those considered never to have been logged or cultivated in modern history (> 500 years; see Denslow & Guzman, 2000; DeWalt *et al.*, 2003). Forest age varied on a fine scale within our subregions (Pyke *et al.*, 2001), so our categorization of age class should be considered to reflect only the dominant relative age of the forests within each subregion.

Forest area and fragmentation

We classified subregions with regard to forest area on the basis of the total area of forest present in each subregion. However, since previous surveys showed a strong effect of fragment size on avian species richness (Robinson *et al.*, 2004), we assumed that the size distribution of remaining patches within a subregion could influence total richness within a subregion. Therefore, we also calculated the proportion of forest included in the one or two largest remaining fragments (degree of fragmentation), in order to evaluate the effect of having the total habitat in a subregion included in several small fragments vs. one or two larger fragments. All data were obtained from Landsat ETM satellite maps showing the normalized difference vegetation index (NDVI) for the years 1999 and 2003 to ensure adequate coverage of all subregions (provided by ACP and ANAM, Panama). We merged the data maps with subregion boundary maps in ARCMAP to calculate the area of forest and other land uses present in each subregion.

Forest bird surveys

Focal species

Although we surveyed all bird species present, this study focuses on resident forest-dwelling species. Species richness in forests is extremely high (Condit *et al.*, 2001) and forests are the most likely habitat to be degraded or destroyed in the study area due to development expansion (Robinson *et al.*, 2004). Following Robinson (1999; see also Robinson *et al.*, 2004), habitat associations of each species were classified into one of the four following categories: forest, edge, open habitats (grasslands, aerial species) and aquatic habitat (see also Ridgely & Gwynne, 1989). 'Forest species' are those detected in both primary and secondary forests. 'Edge species' are those found primarily along the boundaries of forests, with clearings, water bodies or other more open areas. Species inhabiting the top of the forest canopy were also classified as edge species because they occur at the interface between the forest canopy and open air. These include species that occur along other types of forest edge, and species on the wing above the forest canopy (e.g. swifts and vultures). Nevertheless, not all canopy-dwelling species occur along edges; those forest canopy species were

Table 2 Characteristics for the 32 subregions covering the lowland rain forest of the canal corridor, Panama. Details on sources for each variable are detailed in Table 1. Data for plant richness result from interpolation by kriging from surveys conducted by Pyke *et al.* (2001) (see text for details). Topo means topographical complexity; Snst (avrg) means average sensitivity scores from bird species observed in each region.

Region*	Total area (km^2)	Forest cover (%)	Degree fragment (%)	Annual precipitation (mm)	Elevational variability (m)	Topo	Age	Plant richness	Bird richness	Snst (avrg)
1	19.1	33.5	43	1525	101	1	1	52†	18	4.08
2	18.9	5	17	1400	162	2	1	50†	20	4.45
3	4.4	34.2	65	1650	120	1	1	53†	34	4.68
4	36.2	39.2	78	1800	341	3	2	53†	69	5.65
5	106.7	50.6	88	1890	237	3	2	55	86‡	5.88
6	78.6	43	80	2100	178	3	2	67†	99‡	6.17
7	52.5	72.2	93	2300	295	4	3	79	87‡	5.99
8	28.2	91	99	2300	309	5	3	72†	89	6.16
9	46.9	2	65	1633	180	1	1	52†	6	3.92
10	54.7	32.2	66	1770	252	2	1	55†	57	5.56
11	55.7	46.2	78	1935	238	3	2	57†	93	6.24
12	66.9	83.1	96	2200	202	4	3	61	124	7.02
13	20.1	84.4	98	2250	208	3	2	76	111	6.71
14	57.3	89.5	99	2450	152	4	3	92	139	7.54
15	58.6	94.8	99	2600	174	4	3	96	159	7.95
16	11.2	85	94	2550	69	2	2	67	88	6.10
17	67.7	44	74	2441	107	2	2	85	97	6.47
18	27.3	15.4	12	2287	312	1	1	87†	35	5.20
19	17.8	47	71	2132	71	1	1	73†	63	5.59
20	40.9	8.7	23	2287	220	2	1	87†	62	5.37
21	158.2	43	64	2132	289	3	1	61†	43	5.46
22	52.7	87.8	100	3250	111	2	2	90†	138	7.33
23	73.4	92	99	3200	149	5	3	94	154	7.79
24	11.6	53.4	91	3100	123	4	2	89	124	7.12
25	101.9	24.7	29	2750	113	3	2	90†	70	5.26
26	91.7	51.4	63	3200	147	4	2	93†	79	5.77
27	159.8	50	65	3100	162	4	2	94†	97	6.62
28	23.8	52	94	3400	43	1	2	94†	71	5.77
29	49.4	57.5	94	3200	98	1	1	92†	69	5.59
30	21.8	35	49	3400	114	2	1	96†	69	5.67
31	17.3	63	81	3000	87	3	2	109†	79‡	5.46
32	111.7	53.7	86	3500	493	5	3	124	137	7.77

*See Fig. 1 for region numbers. Regions 1, 2, 3 and 9 were removed from the analysis (see text).

†Plant species richness obtained via interpolation (kriging).

‡Bird species richness obtained through the use of MMMean.

retained in the analyses. Species using forest streams were classified as aquatic species if they also used lake or riparian sites for foraging, but if all foraging was conducted along streams inside the forest, the species were classified as forest-dwellers.

Methods of surveying

We inventoried bird species between 1998 and 2005 using several methods. Some easily accessible sites were surveyed first, using point counts, spot mapping and *ad libitum* observations. Preliminary data from these surveys in a subset of the subregions studied here were recently published (Robinson *et al.*, 2000, 2004; Condit *et al.*, 2001). In 2004 and 2005, further intensive effort was focused on most subregions where we accessed remote areas to add to existing lists. We used a 'standardized search' method covering all the microhabitats we could locate in each subregion (Fjeldså, 1999; Herzog *et al.*, 2002; Watson, 2003). During standardized searches, an experienced observer walked throughout each site so that secretive species, that might go unnoticed on point counts, could be detected (Verner, 1985; Terborgh *et al.*, 1990; Fjeldså, 1999; Robinson, 1999; Robinson *et al.*, 2000; Herzog *et al.*, 2002; Watson, 2003). This method has been used successfully for rapid assessment of species richness in Neotropical bird communities. Unlike some Amazonian communities (Terborgh *et al.*, 1990), few species limit their vocalizing to a few minutes before or at dawn in Panama (Robinson *et al.*, 2000), which facilitated our ability to enumerate bird communities rapidly. Observations were also made on flowering and fruiting trees to observe hummingbirds or canopy-dwelling frugivores, many of which are difficult to detect during point counts and transect walks (Karr, 1981; Robinson, 1999). Each survey was conducted during the 5-h period of peak song activity, which lasts from 30 min before dawn until 4.5 h after dawn. At each visit, we kept track of all individual birds heard or seen by keeping a running list of the time at which each observation was made and the identity of each species heard or seen. Playback tapes were used for some forest species known to be extremely rare or to have disappeared recently from certain regions (Lynch, 1989; Ridgely & Gwynne, 1989; Condit *et al.*, 2001; Angehr, 2003; Robinson *et al.*, 2004). Since the avifauna of the region is well-known in terms of the vocalizations, complete inventories of species richness were a realistic goal (Robinson *et al.*, 2004).

To objectively define completeness of the inventory and allow for rigorous comparisons of richness among subregions, we used a result-based stopping rule (Watson, 2003). We constructed species-accumulation curves with respect to time spent surveying in each subregion. A survey was considered complete when a plateau was reached on the curve after 20% of the cumulative time spent surveying elapsed without finding any new species (Hayek & Buzas, 1997; Watson, 2003; Robinson *et al.*, 2004). Even though the sample-based stopping rule provides an *a priori* objective way to efficiently standardize the sampling effort among subregions (Watson, 2003), some species can still be overlooked. Therefore, we also used nonparametric richness estimators to estimate bird species richness and evaluate the accuracy of our rule-based efforts.

We used EstimateS (version 7.0; Colwell, 2004) to estimate species richness. Nonparametric estimators provide robust estimations of total species richness by including species not present in any sample (based on the assumption that the greater number of rare species in a sample, the more likely it is that other species are present that were not detected; Colwell & Coddington, 1994; Gotelli & Colwell, 2001; Colwell *et al.*, 2004). To do this, we used the 20-species list method, which is based on creating series of lists of individuals with 20 species in them (Herzog *et al.*, 2002). The cumulative number of species observed is plotted as a function of the number of 20-species lists pooled to produce a curve that approaches an asymptote when all species have been observed. For sparse data sets (subregions with little forest and few forest bird species), we used a 10-species list method (Herzog *et al.*, 2002). To perform the estimation, we chose MMMean tests (Colwell *et al.*, 2004), which provided the most consistent estimates from our field data (see also Herzog *et al.*, 2002).

Bird species sensitivity

The relative sensitivity of each subregion's bird species to habitat change was ranked based on their life-history characteristics and conservation status. We followed Partners in Flight's prioritization process steps to assign sensitivity scores (PIF, 2001). Adding the scores across vulnerability criteria derived a total for each species. A mean was calculated for each subregion according to forest bird species found in that particular subregion. The following vulnerability criteria were used:

1. relative abundance (*Rel*) reflects the abundance of individuals of a species, within its range and within the study area, relative to other species. Data for abundance were taken from Ridgely & Gwynne (1989) and from the authors' own experiences in the field. Relative abundance data were categorized into five groups (Table 3),

2. sensitivity to disturbance (*Snst*) reflects a qualitative measure of vulnerability to human disturbance based on Stotz *et al.* (1996), which appears to be representative for most species we observed in the study area (Robinson & Rompré, personal observation),

3. distribution within the study area (*Dis*) is a measure of distribution for a given species based on the number of subregions in which a species is known to occur,

4. nationally designated degree of threat of endangerment for each species (*Threat*) (UICN, 1999; see also Angehr, 2003).

Details on all criteria are given in Table 3.

Table 3 Categorical thresholds for scoring relative abundance (*Rel*), sensitivity to disturbance (*Snst*), and distribution within study area (*Dis*)

Score	Definition (see text)
Rel score	
1	Species considered common
2	Species considered fairly common
3	Species considered uncommon
4	Species considered rare
5	Species considered patchy
Snst score	
1	Low sensitivity to disturbance
2	Medium sensitivity to disturbance
3	High sensitivity to disturbance
Dis score	
1	Species present in 32–25 regions
2	Species present in 24–19 regions
3	Species present in 18–13 regions
4	Species present in 12–7 regions
5	Species present in 6–1 regions
Threat score	
1	Near threatened
2	Vulnerable
3	Endangered
4	Critically endangered

Statistical analysis

The first part of the analysis was to determine associations between species richness and individual environmental factors. To do so, we conducted simple linear regressions with log-transformed species richness and precipitation to normalize distributions and stabilize variance (Sokal & Rohlf, 2002).

We tested the combined relationship between the environmental variables with the data on bird species richness obtained through the surveys, via structural equation modelling (SEM; Mitchell, 1992; Byrne, 2001; see also http://www2.chass.ncsu.edu/garson/pa765/structur.htm). This tool uses a confirmatory approach to a model by providing a goodness of fit to determine whether the pattern of variances and covariances in the data is consistent with a path model (see Petraitis *et al.*, 1996; Kline, 1998). SEM allows testing of the descriptive ability necessary to compare different path models (Mitchell, 1992). We used the AMOS® statistical package to conduct the path analysis (Analysis of MOment Structures, Byrne, 2001; see also Shipley, 2000). We considered five models based on the variables mentioned earlier that might potentially best explain distribution patterns, and compared them using the Akaike information criterion (AIC). Delta AIC values higher than 2 and high Akaike weights identified the most likely models (Burnham & Anderson, 1998). A goodness of fit chi-square obtained through the path analysis helped verify the fit of each model. This operation evaluates whether a model's covariance is significantly different from the observed covariance matrix (model fit to the data). Our analysis included several variables, and provided high degrees of freedom (up to 19), which may influence chi-square results (high chi-square values indicate poor model fit). Therefore, we used the relative chi-square, which is the ratio of chi-square to degrees of freedom (χ^2/d.f.), as an alternative to provide a more meaningful evaluation. Models with a ratio of three or less were considered an acceptable fit (Carmines & McIver, 1981; Kline, 1998). Finally, species count data (birds and plants) were log-transformed to normalize their distribution. During the preliminary analysis, we observed a strong correlation between forest age and topography ($r_s = 0.79$, $P < 0.001$), so we incorporated this association within the structural equation modelling, which allows the inclusion of correlated independent variables (correlation among the independents must be modelled explicitly).

Our data were spatially structured and spatial autocorrelation (multicollinearity) may be an issue (Rangel *et al.*, 2006). Therefore, we looked at spatial structure of the data at subregion centroids by identifying outliers and spatially autocorrelated variables, based on the program SAM (Rangel *et al.*, 2006). We used Dutilleul's method for corrected, 'geographically effective', degrees of freedom (d.f.*) to adjust for the amount of spatial autocorrelation (Dutilleul, 1993; Hawkins *et al.*, 2005).

RESULTS

Forest bird surveys

The bird inventory data base we constructed contained more than 50,000 bird observations, over 10,000 of which came from the 2004–05 surveys of 55 sites in the 32 subregions. From a total of 533 species reported in the study area (Angehr, 2006), 177 species regularly inhabit lowland rain forest as year-round residents (Robinson *et al.*, 2004). In our surveys, we located 170 of these species; the remaining seven are extremely rare or became extirpated from the area in the last 30 years (Condit *et al.*, 2001; Robinson *et al.*, 2004). Extensive use of playback tapes in sites where those seven species used to occur has not produced any observations in recent years. In addition to the 170 lowland forest bird species, we observed 24 species characteristic of foothill forests, most of them in region 32 (see Table 2). That region is unique in that it connects the lowland rain forest and the extensive area of foothill forests east of the canal corridor. All species observed are listed in Appendix S1 in Supplementary Material.

Nonparametric species richness estimators (MMMeans) revealed that few forest species were undetected by our surveys. In only four of the 32 subregions did our observed measure of species richness fall outside the 95% confidence interval around the estimated species richness (Table 2). We detected an average of 88.2% of estimated richness in those regions. The estimators predicted 1 to 20 additional species which were undetected by us. For the remaining 28 subregions, richness estimators revealed that assemblages were close to being completely recorded. The completeness of those surveys was > 99%.

Distribution patterns

Bird species richness increased dramatically from regions on the Pacific side of the canal corridor to those on the Caribbean side. In Pacific coastal subregions like Farfan (region 1, Fig. 1) we observed 18 forest bird species, whereas in regions such as Achiote North (region 23), 154 species were observed (see Table 2). Simple linear regressions revealed that this increase could be related to several environmental variables, including rainfall (Robinson *et al.*, 2004). Mean annual precipitation was a strong predictor of bird species richness ($R^2 = 0.43$, $P = 0.001$). It was also a strong predictor of plant richness ($R^2 = 0.32$, $P = 0.001$). Bird richness also increased strongly with other environmental factors such as topographic complexity and age of forest ($R^2 = 0.49$, $P < 0.001$ and $R^2 = 0.67$, $P < 0.001$, respectively), but not with elevation variability ($R^2 = 0.006$, $P = 0.67$). Forest area, as expected, was also a predictor of richness ($R^2 = 0.38$, $P = 0.002$). Similarly, the degree of fragmentation (expressed as the proportion of forest cover included in the one or two largest fragments within a subregion) was positively correlated with bird species richness ($R^2 = 0.48$, $P < 0.001$). The latter result was expected even if forest area within the two largest fragments was not strongly correlated with total forest area in a subregion ($r_s = 0.43$, $P < 0.01$), but the increase in the regression coefficient indicates the important role of fragment sizes in influencing richness within subregions with fragmented forests.

Path analysis

We compared five causal models using the AIC (see Table 4). In each model, we included possible effects of unobserved

Table 4 Akaike's information criterion (AIC) of the structural equation modelling multiple regressions for the five models chosen for the path analysis. Path diagrams for models 1–5 are shown in Fig. 2. A ratio chi-square to degrees of freedom (χ^2/d.f.) between 1 and 3 means acceptable fit (see text for details).

Model ID‡	AIC	Delta AIC (Δ_i)	Akaike weight (W_i)	d.f.*	χ^2/d.f.
1	58.64	0.0	0.826	13	2.2
2	61.89	3.3	0.159	11	2.6
3	67.35	8.7	0.011	13	2.9
4	69.19	10.6	0.004	11	3.2
5	77.75	19.1	0.0001	19	2.3

‡Model ID refers to models compared in Fig. 2.

*Geographically effective degrees of freedom.

variables affecting plant and bird species richness. Those 'unobserved variables' that include variance not explained by the models are required in path analyses (Shipley, 2000; Byrne, 2001). We considered an 'unmeasured covariance' between the two unmeasured variables, which is standard in path analysis (Byrne, 2001). Preliminary runs of the path analysis revealed that, log-transformed, species counts were over-dispersed, which caused the goodness-of-fit chi-square values to be too high (not meaningful for comparison). Four regions with extremely low species counts were considered as 'outliers' and were removed from the analysis. These regions (1, 2, 3 and 9; see Table 2), all on the Pacific slope, exerted an unusual influence on model fit. Forest fragments in these regions included shrubby patches alongside urbanized areas which contained very few forest bird species. Running path analysis without these regions provided us with substantially better-fitting models, without major loss in the scope of the analysis. We initially planned to incorporate elevation variability into each model. However, the correlation between elevation and plant richness became non-significant after Dutilleul's correction for spatial autocorrelation, and four of the five initial models did not meet our goodness-of-fit criterion (see Methods for details). Thus we dropped elevational variability from the latter four models. Following these modifications, most of the models fit data appropriately (ratio χ^2/d.f. < 3.2; Table 4).

The best model of the set, based on AIC (Table 4), confirmed the effects of precipitation only on plant richness, which in turn directly affected bird species richness (Fig. 2). Topography and forest age affect bird species richness directly, as well as forest area and degree of fragmentation, independently of other factors. The second best model was very similar to model 1, with added indirect effects of topography and forest age on birds through an effect on plants (Fig. 2). The higher complexity of model 2 was not justified as indicated by the delta AIC well over 2 (Table 4). Models 3, 4 and 5 showed different direct or indirect effects of environmental factors on plants and birds (Fig. 2). Model 5, which is equivalent to a multiple regression (all variables directly associated with birds, but with the incorporation of correlations between certain variables) performed very poorly (delta AIC > 19; Table 4).

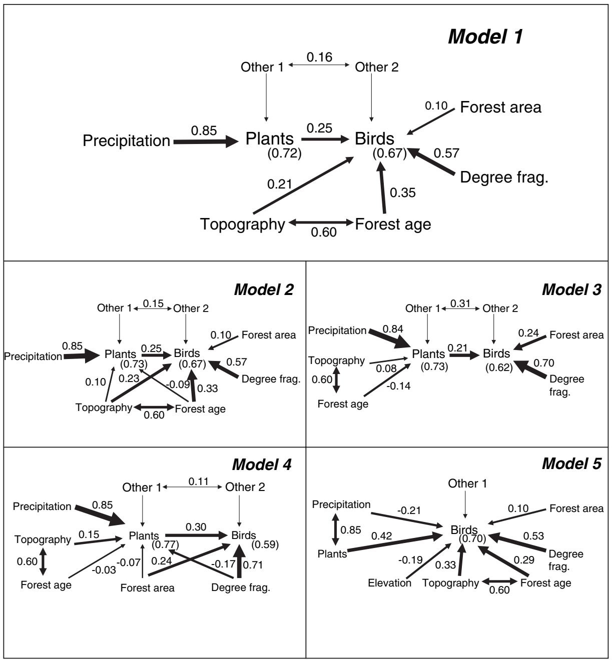

Figure 2 Path diagrams representing the five different structural models we considered to explain distribution patterns for bird species richness in the canal corridor, Panama. The names in the diagram represent the different observed variables in the models: precipitation (mean annual rainfall in mm); elevation (elevational variability in m); topography (topographical complexity); forest age; forest area; degree frag. (degree of fragmentation); plants (plant species richness); birds (bird species richness). Other 1 and 2 represent variation unaccounted for. Arrows represent the relation between variables; the thicker the arrow, the stronger the relation. The numbers on arrows are the path coefficients (standardized regression weights) and numbers in parenthesis (under plants and birds) are squared multiple correlations (total variance explained). Double arrows indicate correlations between variables.

The weaknesses of models 3, 4 and 5 lend support to the hypothesis that some climatic factors affect birds indirectly through their effects on plant species richness while others affect birds directly. Models showing direct effects of environmental variables and forest cover on plants only and indirectly on birds had weak explanatory power (see Table 4).

Species richness and sensitivity scores

Sensitivity scores followed the same patterns as bird species richness, as both were highly correlated ($r_s = 0.98$, $P < 0.0001$). The scores reflect the commonness of the different species in a given region of our study area. Species known to be rare or highly sensitive to habitat change scored between 8 and 16, while common species barely reached a score of 5. For example, a species known to be common in forest understorey, the western slaty antshrike (*Thamnophilus atrinucha*) had a score of 3 (considered common, observed in all regions except Panama City and considered to have low sensitivity to habitat change; Stotz *et al.*, 1996). On the other hand, the harpy eagle (*Harpia harpyja*) reached a score of 16 (considered extremely rare, observed in only three regions, highly sensitive to habitat change and considered nationally threatened and globally near-threatened; Angehr, 2003). All species recorded in this study and their sensitivity scores are presented in Appendix S1. Across most subregions, average sensitivity scores varied between 5 and 6. Fourteen subregions scored higher than 6, while only four scored lower than 5. Those four subregions are located mostly on the Pacific coast, where forests are drier, younger and harbour more common species (Table 2). Regions with a high number of forest bird species held higher sensitivity scores on average, which indicates the presence of more specialized species with limited distribution or even nationally threatened species. Regions that held fewer species were characterized by more common species with lower sensitivity scores. This is the case for regions closer to the Pacific coast, which usually held fewer forest bird species, and included a higher proportion of common and widely distributed species (average scores below 5). On the other hand, regions closer to the Caribbean coast of the study area, which held a high number of forest bird species, included a lower proportion of common species, and a higher proportion of rare species with limited distribution, giving these regions a higher score overall (average score up to almost 8; see Table 2). Forest cover available in each region also affected the score. Regions with little habitat remaining scored low in sensitive species, while regions mostly forested generally scored higher ($r_s = 0.77$, $P < 0.0001$; see Table 2). Additionally, forest bird richness was highly correlated with the number of highly sensitive species within each subregion; $r_s = 0.92$, $P < 0.0001$. Simply put, the larger the area of intact forest, the more species it has, and the greater the number of rare species it has.

DISCUSSION

Climatic and biological factors combined to influence the geographical distribution of bird species richness across the forests of the Panama Canal corridor. Those forests extend 65 km from the Pacific Ocean towards the Caribbean Sea, but experience a steep rainfall gradient and strong changes in plant and bird diversity. We determined, with the help of path analysis, that environmental factors influenced spatial patterns of bird species richness directly, but also indirectly through the effects they have on plant richness. Plant diversity, in turn, could be explained by climatic or environmental factors, which in turn can be explained by underlying geological, pedological and historical factors (Pyke *et al.*, 2001). Thus, while local factors such as plant diversity, topography, forest age and habitat area may directly influence bird species richness, historical and biogeographical factors as well as geomorphological and climatic factors appear to influence bird diversity indirectly. Similarly, the influence of forest age and topography (both correlated) on birds may be better explained via underlying factors such as habitat complexity and food availability.

The humid tropics are often considered to have relatively stable environmental conditions (Rosenzweig, 1995; Hubbell, 2001; Leigh *et al.*, 2004), but our data along with those from an increasing number of studies show that variation in local gradients of moisture availability and other factors greatly affect diversity (Clinebell *et al.*, 1995; Lieberman *et al.*, 1996; Fjeldså *et al.*, 1999; Kessler *et al.*, 2001; Hawkins *et al.*, 2003, 2005; Santiago & Mulkey, 2005; Schnitzer, 2005). In Central Panama, Condit (1998), Pyke *et al.* (2001) and Pérez *et al.* (2005) documented a strong increase in plant diversity as rainfall and the length of the rainy season increase. Robinson *et al.* (2004), based on a coarser and smaller data set, demonstrated a similar pattern of bird species richness with annual rainfall and a strong influence of forest area on species richness. In our study, we confirm this pattern with more bird observations from more sites measured at a finer spatial scale. However, we quantified additional hypothesized factors and found that rainfall and forest area are not the only influential factors.

Structural equation modelling (or path analysis) is a powerful tool for such analyses and is being increasingly used when ecologists want to quantify indirect effects (Mitchell, 1992; Wootton, 1994; Petraitis *et al.*, 1996; Calmé & Desrochers, 1999). This method has been successfully used for modelling drivers of species richness in other species groups and habitats (Grace & Pugesek, 1997; Stevens, 2004). Its specific contribution is to provide a way to understand the individual contribution of each variable within complex systems and to evaluate the relative strengths of direct and indirect interactions among unmanipulated variables (Wootton, 1994; Shipley, 2000). A typical multiple regression model was presented among the path diagrams (model 5) and performed poorly relative to more detailed causal links hypothesized by biogeographical theory. Furthermore, using Dutilleul's (1993) method for geographically effective degrees of freedom allowed our analysis to be robust to spatial autocorrelation (Hawkins *et al.*, 2005; Rangel *et al.*, 2006). From our results, elevational variability was the only factor that did not have a significant influence. One reason for this may be that our study area does not exceed 500 m above sea level, thus limiting the range of values for elevational variability and potentially associated bird communities (Ridgely & Gwynne, 1989; Angehr, 2003).

According to the model most supported by path analysis (see Fig. 2), plant species richness helped predict bird species richness, which in turn was also explained independently by other environmental variables. Therefore, vegetation diversity may play a key role, besides forest age, topography and area, in predicting bird species richness. According to Pyke *et al.* (2001), plant species richness (and composition) is known to be affected by other factors that we did not measure (Pyke *et al.*, 2001; R. Condit, personal communication). Those might be represented by the effects of these unmeasured factors (shown in our path diagrams as 'other' 1 and 2), which explained some of the patterns of plant species richness. Floristic composition is known to be affected not only by precipitation but also by other factors such as geology and biogeographical history. As stated by Pyke *et al.* (2001), the refugial or dispersal hypotheses may explain why we observed higher bird species richness in humid than in dry regions. For example, according to the refugial hypothesis, climate could have oscillated from wet to dry in the past, allowing first the Pacific dry forests to spread north and then Caribbean wet forests to spread south. Alternatively, the dispersal hypothesis proposes that dry forests, under stable climatic conditions, might have established via dispersal from source forests on the Pacific coasts. Nevertheless, there is a predominance of wet forest floristic composition in the canal corridor. This may be the reason why there is a high proportion of forest bird species in so many regions and a higher proportion of sensitive species in wet regions. Our results show that most of the Pacific coast regions had bird species with low sensitivity scores. Four species are known to specialize to dry Pacific coast forests (Robinson *et al.*, 2004), whereas a substantially higher number of species are wet forest specialists (Robinson, 1999; Robinson *et al.*, 2000, 2004).

Not surprisingly, avian diversity along the Panama Canal showed a response to plant species richness, probably because of associated higher vegetation complexity, higher arthropod diversity and diversity of ecological niches (MacArthur *et al.*, 1962; MacArthur, 1964; Terborgh & Weske, 1969; Ricklefs & Schluter, 1993; Siemann *et al.*, 1998; Gillespie & Walter, 2001; Waltert *et al.*, 2003, 2005; Hurlbert, 2004; Tews *et al.*, 2004). Higher rainfall, relating to higher plant diversity in the Panama Canal region, can be a good indicator of ecosystems with a higher productivity (Kaspari *et al.*, 2000; Clark *et al.*, 2001; Hawkins *et al.*, 2003, 2005; Santiago & Mulkey, 2005). Therefore, our results appear to be consistent with the species–energy relationship, although we did not incorporate species abundances quantitatively in our analyses. As stated by Currie *et al.* (2004), increase in energy and species richness is not necessarily followed by increase in abundance of individuals as suggested by species–energy relationships, but may instead reflect an increase in the fraction of rare species. Robinson *et al.* (2000) showed that forest bird communities within the study area are dominated by rare, patchily distributed species. Robinson *et al.* (2004) and our own results from sensitivity scores showed that the wetter Caribbean forest sites have more rare species, which would be inconsistent with predictions of the species–energy hypothesis. In other words, instead of providing more individuals, and therefore more species, our study sites provide a higher proportion of rare species (Currie *et al.*, 2004).

Our results suggest that forest age and topography have a direct influence on bird species richness. In fact, path model 1 reveals a stronger influence of forest age (old-growth forest stands were more readily found in complex topography) then plant richness. Older forests along the Panama Canal are known to be more structurally complex, therefore providing more habitats for animals (DeWalt *et al.*, 2003 and references therein; see also Hurlbert, 2004). One reason why so few forest bird species were found in some of the Pacific subregions is that forests there were very young, and tended to be shrubby (the forest area being actually lower than our mapping method detected) and close to urban areas. This was especially the case for four subregions (including Panama City), which were removed from the analysis. Even so, according to our results, younger forests seemed to harbour fewer forest bird species. In addition, the influence of age and topographic complexity might underlie several other factors, not included in our analysis, which may favour more complex forest bird communities (food availability, competition–predation, interspecific attraction, etc.). In our study area, subregions present on the dry Pacific slope have less diverse plant communities (R. Condit, personal communication, but see Schnitzer, 2005), so we would expect associated bird communities to be composed of more common, generalist species. This is confirmed by the fact that flatter subregions and younger forests feature very few forest bird species. Therefore, our results are consistent with those of Currie & Paquin (1987), Kerr & Packer (1997), Kerr *et al.* (2001) and Rahbek & Graves (2001), which state the importance for biodiversity of topographic complexity and a complex habitat structure. We consider that our study provides better support for the habitat heterogeneity hypothesis, which predicts a positive correlation between species diversity and habitat heterogeneity (see definition in Tews *et al.*, 2004), particularly relevant at local scales (Lavers & Field, 2006). Nevertheless, as mentioned earlier, the relationship between diversity and habitat complexity is also influenced by historical biogeographical events in the region and by habitat area (species–area relationship), confirming that species diversity does not result from a single process (Hill & Hill, 2001; Currie *et al.*, 2004; Ricklefs, 2004).

Currently, all forests in the canal corridor are fragments, ranging in size from 15,020 ha to less than 20 ha. Perhaps the most important result from our study is that resident forest birds were strongly affected by forest area and fragmentation, independently of factors associated with plant species richness. The degree of fragmentation actually had the highest standardized regression weight in most of our path models. This suggests that a fragmentation effect occurs independently from, and with similar strength to, habitat loss *per se*, a situation that has received little empirical support so far (e.g. Fahrig, 2002, 2003 and references therein; see also Betts *et al.*, 2006). Subregions held more forest bird species when forest was represented by one or two large fragments rather than several smaller fragments. However, a fragmentation effect on species persistence may be present only in subregions that have experienced a certain amount of forest loss (Betts *et al.*, 2006; G. Rompré, unpublished data). Evidence for the independent effect of patch size *per se* on bird species richness could have serious implications for conservation efforts. As stated earlier, Robinson *et al.* (2000) showed that most rare and patchily distributed forest-dwelling bird species were present only in large forest tracts. Our results showed that the largest forest tracts held proportionately more sensitive species towards the more humid Caribbean coast.

Compared with species using drier forests, which may be more tolerant to a wider range of precipitation and humidity (Beier *et al.*, 2002; Harris & Pimm, 2004), species highly specialized to wet forest habitats might be less tolerant of habitat change. For example, greater exposure to wind and solar radiation in recently fragmented wet forests creates drier conditions inappropriate for wet forest specialists (Robinson *et al.*, 2004). Caution must therefore be exercised when comparing fragmented habitat in dry vs. wet forests (Beier *et al.*, 2002; see also Harris & Pimm, 2004).

The concentration of species sensitive to habitat loss in large and wet forest tracts should obviously guide conservation efforts, as well as agroforestry and other resource extraction (Terborgh & Weske, 1969; Waltert *et al.*, 2003, 2005). However, our results do not mean that conservation efforts should focus only on the richest forests. Dry forests, even if harbouring fewer forest specialists, may be more at risk at present in the canal corridor (Robinson *et al.*, 2004; Rompré *et al.*, unpublished data). These forest fragments are closer to the country's capital, Panama City, which is inhabited by over 1 million people. For example, young secondary forests are considered to be easier to exploit and, therefore, more suitable for habitat conversion for agriculture or other development (Veldkamp & Lambin, 2001). We need to understand better the socio-economic regulations in use in the canal corridor, and to determine what factors influence and drive human impact and habitat conversion within the study area. Many of the environmental correlates that influence bird distributions probably also affect chances of conversion by humans, and are therefore likely to be useful predictors of future changes in the distribution of bird diversity.

ACKNOWLEDGEMENTS

This study was supported by the National Sciences and Engineering Research Council of Canada, via a PhD fellowship to G.R. Research in Panama was possible thanks to the generous help of the Smithsonian Tropical Research Institute (STRI), Autoridad Nacional del Ambiante (ANAM), Autoridad del Canal de Panama (ACP), Autoridad de la Region Interoceanica (ARI), Centro de Estudio de Accion Social Panameno (CEASPA), Fundo Peregrino Panama (FPP) and Contraloria General de la Republica de Panama. We also thank Elena de Lombardo, Maria Leone, Oris Ovecedo, Benjamen Ordoñez (STRI), Charlotte Elton (CEASPA), Sayda de Grimaldo (ARI), Anjel Muela (FPP), Pascual Fiengo, José and Gladys Isturain for making things easier in the field by giving access and helping coordinate and organize the field work.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Appendix S1. Composition of forest bird communities for the 32 subregions in the Panama Canal corridor.

This material is available as part of the online article from: http://www.blackwell-synergy.com/http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2006.01657.x (This link will take you to the article abstract).

BIOSKETCHES

Ghislain Rompré undertook a PhD in ornithology and forestry with co-directors W. Douglas Robinson and André Desrochers at Université Laval in Québec city, Canada. He also has strong research interests in both temperate and tropical community ecology and conservation biology.

W. Douglas Robinson has research interests in wildlife ecology, particularly relating to songbirds and their conservation, life histories, tropical ecology and aridland ecology. He addresses a variety of questions about the dynamics of ecological systems in natural and modified landscapes.

André Desrochers has research interests in animal ecology, the distribution of animals in natural and human-made landscapes and conservation biology. His long-term objective is to better understand the influence of landscape on habitat selection by wildlife, both during summer and winter periods.

George Angehr is a research associate based at the Smithsonian Tropical Research Institute in Panama. He has research interests in bird conservation in several countries and also serves on the Board of the Panama Audubon Society as Director for Science.

Editor: Bradford Hawkins