Contributed Paper

Testing Hypotheses of Bird Extinctions at Rio Palenque, Ecuador, with Informal Species Lists

DAVID L. PEARSON,* COREY DEVIN ANDERSON,† BRIAN R. MITCHELL,‡
MICHAEL S. ROSENBERG,† RONALD NAVARRETE,§ AND PAUL COOPMANS**††

*School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, U.S.A., email dpearson@asu.edu
†Center for Evolutionary Functional Genomics, The Biodesign Institute, P.O. Box 875301, Arizona State University, Tempe, AZ 85287-5301, U.S.A.
‡Northeast Temperate Inventory and Monitoring Network, National Park Service, 54 Elm Street, Woodstock, VT 05091-1023, U.S.A.
§Fundación Wong, Av. Carlos Arosemena Km 2.5, Guayaquil, Ecuador
**Mindo Cloud Forest Foundation, Condominio Fuente de Piedra 12, San Ignacio N30-50, Quito, Ecuador

Abstract: *Informally gathered species lists are a potential source of data for conservation biology, but most remain unused because of questions of reliability and statistical issues. We applied two alternative analytical methods (contingency tests and occupancy modeling) to a 35-year data set (1973–2007) to test hypotheses about local bird extinction. We compiled data from bird lists collected by expert amateurs and professional scientists in a 2-km² fragment of lowland tropical forest in coastal Ecuador. We tested the effects of the following on local extinction: trophic level, sociality, foraging specialization, light tolerance, geographical range area, and biogeographic source. First we assessed extinction on the basis of the number of years in which a species was not detected on the site and used contingency tests with each factor to compare the frequency of expected and observed extinction events among different species categories. Then we defined four multiyear periods that reflected different stages of deforestation and isolation of the study site and used occupancy modeling to test extinction hypotheses singly and in combination. Both types of analyses supported the biogeographic source hypothesis and the species-range hypothesis as causes of extinction; however, occupancy modeling indicated the model incorporating all factors except foraging specialization best fit the data.*

Keywords: bird community ecology, detectability, ecoinformatics, extinction, expert amateurs, occupancy modeling, professional biologists, species monitoring, tropical forest

Comprobación de Hipótesis sobre las Extinciones de Aves en Río Palenque, Ecuador Mediante Listas Informales de Especies

Resumen: *Las listas de especies recabadas informalmente son una fuente potencial de datos para la biología de la conservación, pero la mayoría no son utilizadas por cuestiones de confiabilidad y temas estadísticos. Aplicamos dos métodos analíticos alternativos (pruebas de contingencia y modelos de ocupación) a un conjunto de datos de 35 años (1973–2007) para probar hipótesis sobre la extinción local de aves. Recopilamos los datos de listas de aves recabadas por amateurs expertos y por científicos profesionales en un fragmento de 2 km² de bosque tropical en la costa de Ecuador. Probamos los efectos de lo siguiente sobre la extinción local: nivel trófico, sociabilidad, especialización de forrajeo, tolerancia a la luz, rango geográfico y origen biogeográfico. Primero evaluamos la extinción con base en el número de años en que la especie no fue detectada en el sitio y utilizamos pruebas de contingencia con cada factor para comparar la frecuencia de eventos de extinción esperada y observada en las diferentes categorías de especies. Posteriormente, definimos cuatro períodos multianuales que reflejaron diferentes etapas de deforestación y aislamiento del sitio de estudio y utilizamos modelos de ocupación para probar las hipótesis de extinción individual y combinadamente.*

Ambos tipos de análisis apoyaron las hipótesis del origen biogeográfico y del rango geográfico como causas de extinción; sin embargo, los modelos de ocupación indicaron que el modelo que incorporó todos los factores, excepto la especialización de forrajeo, tuvo el mejor ajuste a los datos.

Palabras Clave: amateurs expertos, biólogos profesionales, bosque tropical, detectabilidad, ecoinformática, ecología de comunidades de aves, extinción, modelos de ocupación, monitoreo de especies

Introduction

The breakup of tropical forest habitats into smaller patches by human activities is an ongoing phenomenon. Formation of isolated patches of once-extensive forest habitat affects biodiversity largely through extinction and lack of immigration (e.g., Robinson 1999). Particular ecological, morphological and distributional characteristics seem to cause some species to go extinct before others in these fragmented habitats (Klaus et al. 2004). Patch size also is a significant factor in how many bird species can survive in a forest remnant (Ferraz et al. 2007); however, efforts to preserve large tracts of forest are expensive and often politically difficult. Alternative plans to make large forest tracts economically feasible, such as dynamic logging, sustainable natural product harvest, and ecotourism, often depend on extensive knowledge of the minimum size of forest patches needed for viable plant and animal populations (Donald 2004). Long-term studies on multiple plots with controls, quantitative monitoring, and experimental manipulation are the best methods to gather reliable data to identify useful spatial and temporal patterns (Ferraz et al. 2007). Such studies would provide the ecological understanding needed to develop management practices that maximize economic use and maintain biodiversity (Tabarelli & Gascon 2005). Unfortunately, few formal research projects of this nature have been conducted.

Even beyond the problems of obtaining robust, long-term data, conservation biologists are faced with other problems that make studies of the sustainable use and conservation of tropical forests difficult. Paradoxically, one of the most significant of these may be a change in basic philosophy (Battalio 1998). A decade-long movement within the field of conservation biology toward professionalization and rigorous science may have unintentionally marginalized a potentially valuable source of data for understanding and planning tropical forest conservation (Pearson & Cassola 2007). Professional biologists now rarely publish descriptive articles, such as species lists, natural-history observations, and range extensions (Walters 2003). Even descriptions of new species are often perceived as a low priority (Wilson 2000). Consequently, these types of basic data now are published primarily by expert amateurs (Leadbeater & Miller 2004; Pearson & Shetterly 2006). Although resurgence in the use of species lists has made these data more acceptable for some conservation studies (e.g., Remsen 1994; De Silva & Medellín 2001; Balmer 2002), data gathered by amateurs frequently do not receive the support of professional conservation biologists. The major reasons for this bias are that informally gathered species lists can be incomplete, irregular, variable in reliability, and difficult to use in robust statistical analyses.

A variety of parametric and nonparametric statistical methods has been elaborated for inferring the probability of extinction from a sighting record (Solow 2005), but almost all these methods assume equal sampling effort among observation periods, an assumption that is rarely met for informally gathered species lists. Although the problem of unequal sampling effort has made informally gathered species lists difficult to use in statistical analyses, all species lists, even those gathered under formal monitoring programs, suffer from the problem of imperfect detection of species. Few animals are so conspicuous that they are always detected at each survey, which makes it difficult to determine how long a species can go undetected before it is considered extinct (e.g., Solow 2005; MacKenzie et al. 2006; Kéry & Royle 2008). Failing to account for imperfect detectability may result in underestimates of site occupancy and biased estimates of local colonization and extinction probabilities. MacKenzie et al. (2002, 2003) propose a model- and maximum-likelihood-based method for estimating occupancy rates when the probability of detection is less than one. This method can be extended to examine changes in community-level occupancy by treating each individual species as a site within the modeling framework. Initial occupancy, colonization, local extinction, and detection probability parameters then can be estimated on the basis of repeated visits during multiple seasons.

We used contingency tests and occupancy modeling to examine alternative hypotheses and corresponding predictions about why some species of birds disappear before others (Table 1). We based our data on species lists collected from one of the last remnants of lowland rainforest in central coastal Ecuador, Rio Palenque. This list of bird species was produced primarily from records of expert amateur bird watchers and professional leaders of bird tours. Our goal was to determine the hypotheses that best explained extinction patterns at Rio Palenque and to explore the relative utility of different methods for testing hypotheses about extinction with informally gathered species lists.

Table 1. General hypotheses and specific predictions tested to explain the disappearance of some bird species before others in a tropical forest fragment at Río Palenque, Ecuador.

	Hypothesis	*Prediction*	*Model ε*[*]	*Model prediction*
Ecological–behavioral factors				
trophic level	Food type will influence extinction (Davies & Lawrence 2000).	The disappearance of species should generally be from highest to lowest in the following order of trophic level foraging guilds: predator, insectivore, frugivore-gramnivore, nectarivore, omnivore.	food specialist	Food specialist will be positive.
social dependence	Complex social behavior causes dependence on conspecifics and sensitivity to population fluctuations (Purvis et al. 2000).	Species with obligatory social adaptations such as colonial nesting, flocking, and leking will disappear before more solitary species.	solitary	Solitary will be negative.
body size	Body size influences territory size, generation time, population density, and probability of extinction (Sodhi et al. 2006).	Physically large species will disappear before smaller species.	body norm	Body norm will be positive.
foraging specialization	Food specialization influences susceptibility and ability to adapt to rapid environmental changes (Haugaasen et al. 2003).	Species adapted to a narrow ecological niche, food type, or microhabitat (e.g., army ant followers, trunk creepers) will disappear before species adapted to a broad spectrum of food or microhabitats (e.g., leaf gleaners, salliers).	specialized	Specialized will be positive.
light level	Anatomical and physiological adaptations to light and associated thermoregulation often limit species to various ambient energy (fragmented) microhabitats (Laurence & Gomez 2005).	Species adapted to low light microhabitats will be more susceptible to increasing energy levels in disturbed forest and disappear before species adapted to moderate to high energy level microhabitats.	low light	Low light will be positive.
Abundance-occupancy factors				
species range area	The reservoir of individuals, genetic variation, probability of dispersal, and local extinction is influenced by the total surface area of a species' geographical range (Hanski 1982; Gaston 1994; Gaston et al. 2000).	Forest species with small geographical ranges will become locally extinct before those with large ranges.	small range	Small range will be positive.
biogeographic source	Disruption of dispersal corridors and habitat availability will differentially affect birds immigrating from and adapted to biogeographic source areas with different physical features (Rosenzweig 1995; Mehlman 1997).	Species that evolved in forest of relatively high and constant moisture, low seasonal fluctuations (Chocó), or higher elevation (montane cloud forest) will disappear before species originating in more seasonal and drier forests at an elevation similar to that of Rio Palenque (broad biogeographic area origin).	not broad	Not broad will be positive.

[*]*Explanation: food specialist, any guild other than omnivore; solitary, species that is not colonial, flocking, or leking; body size, normalized body length; specialized, species that is predominantly an army ant follower, trunk or branch creeper, or predatory pouncer; low light, species limited to forest floor, undergrowth, midstory, or subcanopy; small range, species whose geographical range has a total area of 1 million km² or less; not broad, species whose biogeographic origin is cloud-montane forest, Chocó, disjunct, or Tumbesian.*

Methods

Study Site

The Rio Palenque Scientific Center (RPSC) is a private reserve of 208.87 ha, of which 115.51 ha are protected as intact lowland forest. Established in 1971, this reserve is owned and managed by the Fundación Wong of Guayaquil. The RPSC is located in central coastal Ecuador, along the Río Baba in the northern part of the province of Los Ríos (0.59°S; 79.38°W). Elevation in the reserve ranges from 130 to 190 m. The forest is categorized in the Holdridge system as humid lowland rainforest with transition to very humid premontane forest.
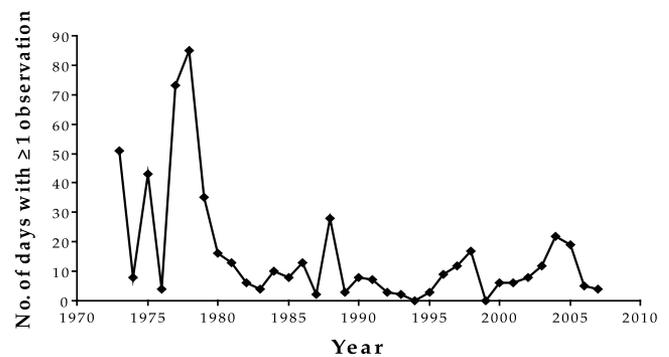
The flora and avifauna of the RPSC reflect its location at the junction of at least three distinct biogeographic regions. The extreme southern extent of the lowland humid tropical rainforest and subtropical rainforest of the Chocó ecoregion reaches the Rio Palenque reserve. The distinct Tumbesian ecoregion is typically drier and extends north from coastal Peru into Ecuador where it reaches its northern limit in the Rio Palenque area. Finally, the Andean slopes and higher elevation biota descend west into the area seasonally or sporadically, especially along finger-like ridges.

Three major steps of human-caused habitat change occurred in and around the RPSC over the last 40 years: in the late 1960s and early 1970s parts of the native forest began to be cut and cleared around the RPSC; until the early 1980s, narrow corridors or relatively short distances through plantations connected the RPSC to many small adjacent forest patches; by the early 1990s, the last of these peripheral remnant patches of native forest were replaced by agriculture and the RPSC became an isolated fragment of native forest.

Species List

O. Owre, F. Sibley, and their students made the first inventory of bird species in the RPSC in 1971. A decade later, Leck (1979) and his associates (Leck et al. 1980) published updates of the avifauna. From 1972 to 2007, ornithologists, expert amateur birdwatchers, and leaders of bird ecotours supplemented the records with unpublished observations and informal reports.

R. Navarrete and F. Man-Ging compiled a list of bird species recorded from RPSC from a combination of published lists and informal notes deposited at the station. We filtered the deposited bird lists by judging them for accuracy and possible mistaken identifications. To better focus on the extinction impact on forest bird species, we deleted from the analysis aquatic and secondary habitat species and boreal and austral migrants. For species interpretations, we followed Ridgley and Greenfield (2001*a*, 2001*b*). Details of the ecological, morphological, and biogeographic categories we used for analysis are available (see Supporting Information).

Figure 1. Sampling effort at the Rio Palenque Science Center from 1973 to 2007, measured as the number of days per year in which at least one bird species observation was recorded.

Contingency Tests

Because sampling effort varied (Fig. 1), most standard methods for inferring extinction were not applicable. We applied several ad hoc methods for determining whether or not a species was present at the end of the sample period. First, the data set was partitioned within buffer periods at the end of the sample period (range 4–7 years). If a species was not observed within the buffer period, it was considered extinct. Alternatively, species were considered extinct if they had not been observed for at least 5 years and the average gap length between observations of that species over the sample period was less than the number of years since the species had last been observed. Although the fact or time of local extirpation of a bird species cannot be absolutely known, the small size of the fragment, the extensive field experience of many of the observers, and the established use of playback of sound recordings (Boscolo et al. 2006), particularly toward the end of the study period, increased the chances that the lack of observation of a species over several years at the end of the study represented local extirpation.

For each hypothesis and corresponding prediction in Table 1, the number of species that went extinct and the number of species that persisted within each category were compared with random expectations in contingency tests (chi-square goodness-of-fit test or Fisher-Freeman-Halton exact test, depending on sample size). All contingency tests were conducted with the StatsDirect software package (StatsDirect, Chesire, United Kingdom).

Occupancy Modeling

To test more rigorously the relative strengths of the hypotheses in Table 1, we developed a series of multiseason occupancy models in PRESENCE (Hines 2006) following MacKenzie et al. (2006). This approach explores community-level occupancy by treating each individual species as a site within the modeling framework. It then

estimates initial occupancy (ψ), colonization (γ), local extinction (ε), and detection probability (ρ) parameters on the basis of repeated visits during multiple seasons. This modeling framework assumes the community is "closed" within a season and that colonization and local extinction of species only occur between seasons (MacKenzie et al. 2006).

Initially, we assumed the Rio Palenque bird community was closed during three multiyear time periods ("seasons") that reflect different stages of isolation of the study site: (1) 1975 and earlier, when the site was continuous forest with numerous small clearings around the border; (2) 1976–1982, when there were large clearings surrounding the site but large forested corridors were still present; and (3) 1983 and later, when corridors were severely reduced and the main forest fragment at Rio Palenque was isolated by field crops, banana, and African palm plantations. For the analysis, however, we divided the third period into two "seasons" (1983–1994 and 1995–2007) because data were sufficient to support a four-"season" model, and we considered 24 years too long for the assumption of community closure.

Although our primary interest was to examine hypotheses affecting the local extinction parameter, we also developed a null model that included covariates for occupancy, colonization, and detection probability. These additional covariates helped reduce the risk of bias in parameter estimates due to unmodeled heterogeneity (MacKenzie et al. 2006). We modeled occupancy as a function of range size and biogeographic distribution (not broad, broad); colonization probability as a function of time (t), range size, and fragmentation tolerance (forest edge or shaded foliage-use species); and detection probability (P) as a function of sampling effort (days of surveys per year), body size, whether or not the species forages in the forest canopy, and whether or not the data were from after 1994 (when audio playbacks were used more often). In addition, extinction probability was always allowed to vary as a function of time (Table 2). In the typical notation for occupancy models our null model was ψ(small range + not broad) $\gamma(t$ + small range + fragment tolerant) $\varepsilon(t)$ P(effort + small body + not canopy + playback) (some variables defined in Table 2).

To estimate the impact of improved technology in detectability of bird species over the last period, we also conducted our analysis without the playback parameter. We then developed models of ε on the basis of a priori hypotheses by choosing one variable that best represented each hypothesis (Table 2). Next, we built additive, interaction, and modified interaction models to explore the effect of our variable. In the additive model, the variable had the same effect on extinction rate between each time period, whereas in the interaction model it had a different effect between each time period. For the modified interaction model, we removed an instance of the variable from the interaction model whenever the

Table 2. Null model parameters and variables for occupancy analysis of causes of local forest bird extinction over 35 years at Rio Palenque, Ecuador.

Parameter	Variable	Description
Ψ	small range	1 if species range l $\leq$ 1 million km^2, otherwise 0
	not broad	1 if species not broadly distributed, otherwise 0
γ	T	Different intercept for each transition between "seasons"[a]
	small range	1 if species range <1 million km^2, otherwise 0
	fragtol	1 if species is fragmentation tolerant[b]
ε	T	Different intercept for each transition between "seasons"
P	effort	Days of surveying effort per year, divided by 10
	small body	1 if body length <30 cm, otherwise 0
	not canopy	1 if primary foraging location is not the canopy, otherwise 0
	playback	1 if after 1994

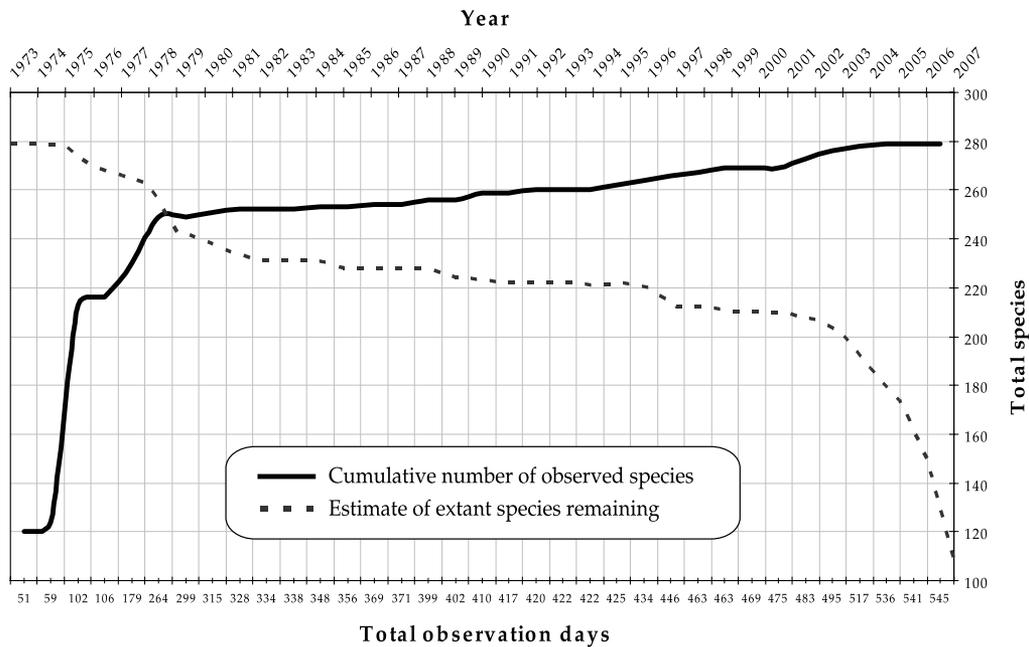[a] *Seasons are periods of years:* $\leq$*1975; 1976-1982; 1983-1994; 1995-2007.*
[b] *A species is fragmentation tolerant if it occurs on forest edge or over a wide range of foliage types.*

parameter estimate was smaller than its standard error. We used the information–theoretic approach to compare the best model with the other best models and the null model (Burnham & Anderson 2002). The models for each hypothesis did not necessarily test the specific predictions of the hypothesis; they only indicated whether the variable chosen to model ε was better than other models at explaining the data. Nevertheless, examining the pattern and magnitude of parameter estimates invariably provided additional insight into the validity of our predictions.

To determine the best model, we applied Akaike's information criterion (AIC), which is a relative measure of the information lost when a given model is used to describe reality. When the results of multiple models derived from the same data set are compared via AIC, the model with the lowest AIC is the best model or the one closest to the data's true generating mechanism.

Our approach was suitable for identifying the best single model of ε on the basis of the set of extinction hypotheses, but it did not account for the possibility that a model derived from multiple hypotheses acting together would be even better. Therefore, we also produced a global model that incorporated the best model for each hypothesis. For our final ("best") model we removed any parameters for which the estimate was smaller than its standard error.

Occupancy modeling can also produce estimates of "relative species richness," which is the expected number of species present on the basis of the model and a list of potential species that are known to occur in the area. The list we used was the number of nonmigratory,

Figure 2. The cumulative number of nonmigratory, forest-associated bird species added to the Rio Palenque Science Center species list annually (solid line) compared with the cumulative annual number of species lost (dashed line) under the extreme assumption that the last year a species was observed represents the year it became extinct.

forest-associated species detected over the course of the entire study. The calculation for a given period of years or "season" is the number of species detected plus the sum of the predicted occupancy of all species not detected (Dorazio & Royle 2005; MacKenzie et al. 2006). We also calculated 95% confidence intervals for the richness estimates (with CIs for individual species that were not detected), and we calculated relative species richness for subgroups, such as ecologically or biogeographically similar species.

Results

The list of bird species included 413 verified species of 54 families. Thirty species were boreal and austral migrants (7%) that were present only part of the year. One hundred one species (24%) had not been recorded on the reserve since 2003, and of these species 59, 26, and 15 were last observed between 1972 and 1980, 1981 and 1991, and 1992 and 2003, respectively. Seventy four (73%) were forest-associated species. Twenty-six species were added to the list since 2000, but of these only nine were forest-associated species. Of the 59 species endemic to the Tumbesian biogeographic area of southwestern Ecuador (Ridgley & Greenfield 2001*a*), 24 (41%) occurred at RPSC. Sixteen of the 31 species (52%) endemic to the Chocó biogeographic region and occurring in northwestern Ecuador occurred at RPSC (a complete

bird species list and their categories are available from http://www.rosenberglab.net/supplements.php).

For statistical analyses we included only nonmigratory and locally migratory, forest-associated bird species recorded at RPSC from 1973 to 2007. Of the 277 species that met these criteria, approximately 90% had been recorded by 1980 (Fig. 2). On average, species were observed 10 times over the study period (median = 9), and there was an average of three years (median = 2) between observations when there were years in which a species was not observed. Many species observed in the first decade of sampling were not reported subsequently. When we used 4- to 7-year buffer periods at the end of the study period, the number of nonmigratory, forest-associated bird species that were considered locally extinct ranged between 76 and 65 (respectively). When average observation gaps were used to infer extinction with a 5-year minimum buffer period, 69 nonmigratory, forest-associated bird species were considered locally extinct.

In contingency tests the trophic-level and biogeographic source null hypotheses were rejected consistently. More montane species and Chocó region species were extirpated than expected, whereas more broadly distributed species persisted than expected (Table 3). More fruit and seedeaters and predatory species were extirpated than expected; however, more generalists persisted than expected (Table 3). For the range-size hypothesis, the null hypothesis was rejected for all buffer periods between 4 and 7 years, but could not be rejected at the

Table 3. Results of contingency test for the biogeographic-source hypothesis and the trophic-level hypothesis[a] that compares the observed and the expected number of species that were extirpated and persisted within different categories.

Hypothesis	Variable	Extirpated		Persisted	
		observed	expected	observed	expected
Biogeographic source[b]	broad	44	56.24	161	148.75
	Chocó	11	4.93	7	13.06
	disjunct	3	3.57	10	9.43
	montane	13	4.93	5	13.06
	Tumbesia	5	6.31	18	16.69
Trophic level[c]	fruits-seeds	16	10.97	24	29.03
	omnivore	13	17.83	52	47.17
	insects	23	32.65	96	86.35
	nectar	11	7.13	15	18.87
	predator	13	7.41	14	19.59

[a] *Due to small sample sizes in some cells, a Fisher-Freeman-Halton exact test was used for the biogeographic-source hypothesis, whereas a chi-square goodness-of-fit test was used for the trophic-level hypothesis.*
[b] $p \leq 0.0001$.
[c] $p = 0.0015$.

0.05 level when extinction was estimated on the basis of average gap lengths. More species with small ranges were extirpated than expected, whereas more species with large geographic ranges persisted than expected. The null hypothesis was also rejected for the body-size hypothesis with a buffer period of 4 years, but p values were less significant statistically for other partitions; more large species were extirpated than expected, whereas more small species persisted than expected.

Of the occupancy models addressing only a single extinction hypothesis, the most-supported was the biogeographic-source hypothesis (Table 4); the next best single-hypothesis model was species range ($\Delta AIC = 30$). A $\Delta AIC > 10$ indicates virtually no support for the model with the larger AIC (Burnahm & Anderson 2002), so none of the remaining single-hypothesis models was likely to

be the best model in the set. Nevertheless, there was clear support for the conclusion that several of the hypotheses act together to influence local extinction rates. The AIC of the global model (all seven hypotheses) was approximately 20 units lower than that of the model of the biogeographic-source hypothesis (Table 4).

Removing the weakest hypothesis, foraging specialization, resulted in a best model that was a slight improvement over the global model ($\Delta AIC = 1.37$, Table 4). When removing a parameter results in only a slight change in the model deviance (log likelihood times -2 or -2log likelihood), the model with the extra parameter is not supported and can be ignored (Burnham & Anderson 2002). Even though the foraging specialization hypothesis was a slight improvement over the null model, it appeared to be the only hypothesis of the seven

Table 4. Comparison of competing occupancy models of local extinction (ε) of bird species on a lowland forest fragment in coastal Ecuador, Rio Palenque.

Model[a]	AIC[b]	ΔAIC[c]	Number of parameters[d]	Deviance[e] (-2 log likelihood)
Best model (global minus specialized$_2$)	9118.41	0.00[f]	26	9066.41
Global model	9119.78	1.37[g]	27	9065.78
Biogeography (not broad$_1$, not broad$_2$)	9138.92	20.51	18	9102.92
Range (small range)	9166.51	48.10	17	9132.51
Social dependence (solitary$_1$, solitary$_2$)	9172.41	54.00	18	9136.41
Light level (low light)	9175.62	57.21	17	9141.62
Size (body norm$_1$, body norm$_2$, body norm$_3$)	9176.28	57.87	19	9138.28
Trophic level (food specialized$_2$)	9177.74	59.33	17	9143.74
Foraging specialization (specialized$_2$)	9180.61	62.20	17	9146.61
Null model	9180.78	62.37	16	9148.78

[a] *See Table 1 for definitions of model parameters. Subscript numbers after a model or variable name indicate an interaction model was the best model for the hypothesis and denote the time-period transitions (1, $\leq$ 1975; 2, 1976–1982; 3, 1983–1994; 4, 1995–2007) in which the variable was retained in the final model. Lack of a subscript after a variable name indicates the additive model was the best model.*
[b] *Akaike's information criterion. Among competing models, the one with the lowest AIC is the best.*
[c] *Difference between the AIC of the model and the AIC of the best model.*
[d] *Used together with deviance to calculate AIC.*
[e] *Log likelihood times -2.*
[f] *AIC weight = 0.6648.*
[g] *AIC weight = 0.3351.*

Table 5. Best-model parameter estimates of local extinction compared with predictions (See Table 1 for definitions of parameter variables) at Rio Palenque, Ecuador.

Hypothesis	Variable[a]	Estimate (SE)[b]	Prediction
Trophic level	food $spec_2$	0.87 (0.57)	positive[c]
Social	$solitary_1$	−0.81 (0.57)	negative[c]
dependence	$solitary_2$	1.00 (0.43)	negative
Body size	body $norm_1$	−0.72 (0.51)	positive
	body $norm_2$	0.33 (0.19)	positive[c]
	body $norm_3$	0.88 (0.31)	positive[c]
Light level	low light	0.81 (0.32)	positive[c]
Range size	small range	0.73 (0.38)	positive[c]
Biogeography	not $broad_1$	2.64 (0.67)	positive[c]
	not $broad_2$	1.57 (0.44)	positive[c]

[a]*Subscript numbers after a variable name indicate an interaction model was the best model for the hypothesis and denote the time-period transitions (1, ≤ 1975; 2, 1976-1982; 3, 1983-1994; 4, 1995-2007) in which the variable was retained in the final model. Lack of a subscript after a variable name indicates the additive model was the best model.*
[b]*Estimates represent the change in logit(ε) due to the presence of an indicator variable (e.g., solitary as opposed to nonsolitary). For body norm, it is the change in logit(ε) due to an increase of 1 SD (13.6 cm) of body length.*
[c]*Predictions supported by the model.*

that was not important at Rio Palenque when all hypotheses were considered together in a global model.

When our null hypothesis with audio playback included was compared with tests without it, the playback parameter was important for modeling detection probability (ΔAIC between models with and without the parameter exceeded 450 units). The other estimates, however, were nearly identical (often to two decimal places), and they had virtually overlapping CIs. Thus, the inclusion of the playback parameter did not affect the estimates of occupancy, colonization, or local extinction. This pattern suggests our analysis was robust to changes in the specific parameters of the null model.

We then examined the parameter estimates of the best model to explore whether the predictions of the different local extinction hypotheses were supported consistently throughout the study period. The hypothesized differences in extinction rates were not operating with the same strength at all times throughout the 35 years, otherwise the additive models would have been the best for all hypotheses. Rather, in most cases the presence, magnitude, and sometimes direction of the local extinction variables changed depending on the transition period being modeled (Table 5). The trophic-level hypothesis did not operate between the first and second time periods, a transition from intact forest to connected patches. All six hypotheses (other than foraging specialization) were operating between the second and third time periods, a transition from connected patches to isolated forest. Only three hypotheses were active during the last transition,

Table 6. Relative species-richness estimates (95% CIs) over four "seasons" (multiyear periods) for species presumed tolerant or intolerant of fragmentation.

"Season" (years)	All species[a]	Fragmentation tolerant[b]	Fragmentation intolerant[b]
<1975	266 (258–272)	88 (85–89)	179 (173–182)
1976–1982	262 (256–268)	88 (86–89)	174 (170–179)
1983–1994	238 (224–252)	84 (81–88)	153 (142–164)
1995–2007	262 (255–268)	88 (86–90)	174 (169–179)

[a]*From the list of 277 nonmigratory and locally migratory forest-associated bird species recorded at Rio Palenque Scientific Center.*
[b]*Forest edge and canopy specialists and generalists were considered fragmentation tolerant; forest floor, undergrowth, midstory, and sub-canopy specialists were considered fragmentation intolerant*

when the forest was isolated. In most cases, the direction of the effect was as predicted. Exceptions were the social-dependence hypothesis between the second and third time periods and the body-size hypothesis between the first and second time periods.

On the basis of the list of 277 species and output from the best model, we calculated that the relative species richness during the first, second, third, and fourth periods was 266, 262, 238, and 262 (respectively) (Table 6).

Discussion

Although the efficacy of the ad hoc contingency test methods we used to infer extinction are debatable (Moore & Swihart 2007), our results were generally consistent across tests regardless of the buffer period applied.

We found general support of study predictions among species categories with nonrandom cell frequencies. For example, results of contingency tests for the biogeographic-source hypotheses indicated more montane species and Chocó region species disappeared than expected, with the deviation from random expectations being larger for montane species. On the other hand, more broadly distributed species persisted than expected by chance. These results are consistent with the prediction that montane species would be the first to disappear, species in the Chocó region would be second, and broadly distributed species would be the least susceptible to extirpation. We based this prediction on the assumption that montane species are adapted to high elevations, but sometimes migrate to low elevations when resources are limited (Powell & Bjork 1994). Because most dispersal corridors connecting RPSC to montane habitats were eliminated by the early 1980s, montane species were expected to be among the first to disappear. Elimination of forested corridors was also predicted to affect species associated with lowland humid tropical rainforest and subtropical rainforest of the Chocó region; however, because of broader corridors and similar habitat and elevation, the

impact was predicted to be less severe than that experienced by migratory montane species.

Contingency-test results were generally consistent with the predicted order of disappearance of species categories for the trophic-level hypothesis. Nevertheless, more frugivores and seedeaters disappeared than expected, whereas more insectivores persisted than expected. This result runs counter to the prediction that insectivores would disappear before frugivores and seedeaters. Although frugivores and seedeaters may consume food resources from a wide variety of sources, preferred resources are often widely distributed spatially and temporally. The availability of such resources may have been lessened as dispersal corridors connecting RPSC to other forest patches were eliminated, and available habitat within RPSC was reduced. It is difficult to explain why more insectivorous species persisted than expected, but perhaps unique weather patterns, such as irregular but strong impacts from El Niño events (Rodbell et al. 1999), had greater influence on flowering and fruit set than on insect abundance (Wright et al. 1999).

Contingency-test results were also consistent with the prediction that species with small geographic ranges would be more susceptible to extinction than species with large geographic ranges. There was some evidence that large-sized species were more susceptible to extinction than small-sized species, but contingency test results were only significant for a 4-year buffer period. Ideally, both range size and body size should be treated as continuous variables and tested for correlation with time of extinction, but this was not feasible with the RPSC species list.

The contingency-test results were similar to those inferred by the more rigorous occupancy–modeling approach, perhaps due to the absence of strong patterns in detection probability across the groups of species being compared. The most strongly supported of the single-hypothesis occupancy models was the biogeographic-source hypothesis. The species-range hypothesis was in second place. Nevertheless, the model that incorporated all hypotheses except the foraging-specialization hypothesis was the most strongly supported. This finding reemphasizes the point made by previous authors (Pearson 1977, 1982) that many of the individual hypotheses and their predictions may not be mutually exclusive. For example, large body size is often associated with large territory size, small population size, and slow reproductive rate. Thus, our results suggest that single-factor analyses (such as contingency tests) may have the power to identify hypotheses that are strongly supported by the data, but they lack the power to discriminate among multiple, interacting hypotheses.

Another advantage of the occupancy-modeling approach is that model parameters can be examined to determine directionality of predictions and generate causal questions and hypotheses that otherwise might not have been evident (Table 5). For instance, body size showed a changing trend of apparent extinction of large bird species with increasing forest fragmentation. Perhaps initially these large species can move more easily among areas with moderate fragmentation than small species. As fragmentation increases, however, the gaps become less and less trivial, and larger species may have a disadvantage in later time periods because of their greater habitat needs. For the social-dependence hypothesis, it is possible that there are two groups of social species. One subset of species within this group was sensitive to extinction and actually tended to become locally extinct between the first and second time periods. Then, between the second and third time periods, this left a group behind whose sociality better buffered them from extinction (perhaps due to cooperation in the face of adversity). Thus, between the second and third time period, solitary species did relatively worse than the remaining social species.

In the third period many forest-interior species disappeared, especially forest floor, undergrowth, midstory, and subcanopy specialists (Table 6). Nevertheless, the rebound in expected species richness in the fourth period appeared to be due to recolonization by some of these same species.

Additional differences in results from the contingency analysis and the occupancy model may be due to differences in the time periods we used. Furthermore, the contingency method did not adjust for sampling effort or other sources of heterogeneity among years. When the raw data were summarized, the model mirrored the pattern of sampling effort (similar numbers of species in the first, second, and fourth time periods, with a dip in the third time period, see Fig. 1). This relatively new application of occupancy modeling for estimates of local species extinction suggests that it may be useful in dealing with complicated data sets, but that its usefulness is also constrained by the vagaries of effort and reporting inherent to informally collected data sets.

Furthermore, the results of occupancy modeling could be biased by violation of the assumption of closure if species colonized or become locally extinct within a "season" rather than between "seasons" (Kendall 1999). Although occupancy estimates would be biased by nonrandom violations of the closure assumption, it is not clear how estimates of colonization and local extinction would be affected.

In general, results from a single site are limited in their usefulness for defining broad ecological patterns and incorporating policy for forest management and conservation. In addition, irregular climatic events may influence extirpations in many if not most tropical forest sites (Wright et al. 1999). Nevertheless, without constant monitoring of populations and individuals, dispersal and immigration into and from intact forest sites may make these extirpations difficult to detect.

The results of our study highlight the potential utility of informatics-oriented approaches for studies of biodiversity and conservation. The emergence of online public databases for storing species observations will increase the frequency of this type of data and will make them more accessible for scientific analysis. Rather than ignoring these data because they are not collected in a rigorous manner, researchers should consider what information can be inferred that might be useful in developing management and conservation policy. By determining the limitations of species observations, researchers can identify ways in which amateur naturalists and database managers can most easily improve data collection to maximize statistical inference.

From contacts with tourist lodges, government agencies, private nature tour companies and NGOs, we estimate that there are 20–50 additional sites in tropical forests around the world with extensive bird lists and similar detection–nondetection data for each species. Some of these sites have data from as early as the 1960s and 1970s. Comparisons of bird species extirpation patterns for these sites would allow a broader array of statistical tests with more sophistication and power. With data from intact sites, larger or smaller forest fragments, similar bird communities or different bird communities, sites buffered from anomalous weather events and those exposed to hurricanes, droughts, and flooding, many more predictions and tests are possible. These predictable subsets of surviving species groups (nestedness) are likely to prove useful in determining community ecology patterns and improving conservation efforts of forest fragment birds (Mac Nally et al. 2002; Martínez-Morales 2005). Eventually, comparative data on species lists of amphibians (Vigle 2008), reptiles, mammals, plants, and other nonavian taxa (Escobar et al. 2008) would provide even more useful comparisons and more robust conclusions and generalizations.

Acknowledgments

Supporting Information

Criteria for hypotheses testing used in Table 1 are available as part of the on-line article (Appendix S1). The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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