Special Issue Article: Tropical Insectivores

Ongoing changes in the avifauna of La Selva Biological Station, Costa Rica: Twenty-three years of Christmas Bird Counts

W. Alice Boyle [a,*], Bryan J. Sigel [b]

[a] Division of Biology, 116 Ackert Hall, Kansas State University, Manhattan, KS 66506-4901, USA
[b] Department of Biology, Nevada State College, 1121 Nevada State Drive, Henderson, NV 89002, USA

ARTICLE INFO

ABSTRACT

Tropical forest fragmentation influences community composition via differential species-level effects. Avian responses to fragmentation at La Selva Biological Station are, in part, responsible for the particular concern over the fate of understory insectivorous species. However, since the 1990s, much previously deforested land within and surrounding La Selva has reverted to forest, providing an opportunity to test hypotheses explaining ongoing avifaunal change. Analyses of 23 years (1989–2011) of Christmas Bird Counts reveal that 63 of 202 species have increased whereas 44 are declining, with declines occurring more rapidly than increases. Habitat association was an important predictor of population trends, as understory birds continue to decline whereas forest generalists increased. Our results differ from previous work in the tropics by revealing that, at La Selva, insectivores are not currently suffering greater declines than birds of other dietary guilds. Instead, body size was more strongly associated with population change than was diet, with smaller birds having more negative population trends than larger birds. These results suggest that we must consider additional hypotheses that may explain ongoing population declines of tropical birds. In particular, the associations between population trends and body size implicate physiological mechanisms influencing population change, which may result from direct or indirect consequences of changing climates.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

Anthropogenic habitat loss and forest fragmentation are the primary causes of the current global biodiversity crisis. Destruction of tropical forests is a critical problem because these habitats harbor much of the world's biodiversity (Dirzo and Raven, 2003; Gibson et al., 2011). Biodiversity loss occurs even in relatively large forest fragments (Laurance, 2008; Saunders et al., 1991), yet the reasons why some species are able to persist and others become extirpated from fragments is still poorly understood. Extirpations from fragmented landscapes mirror many of the processes governing patterns of biodiversity in island systems (Fahrig, 2003; Turner, 1996); area and isolation influence the probability of local extirpation and the chances of recolonization via dispersal (MacArthur and Wilson, 1967; Rosenzweig, 1995). Landscape-level factors are also known to affect species persistence in fragments, such as distance from source populations, the nature of the non-forested matrix, and the connectivity of fragments. These factors influence the ability of mobile organisms to recolonize fragments (Haddad and Tewksbury, 2005; Ricketts, 2001). Consequently, species-level attributes influencing extirpation risk are often related to home range size (Terborgh et al., 1990), which determines the maximum population size in a fragment of a given area. Large home ranges are characteristic of animals with large body size, high trophic position, and specialized foraging requirements (Gompper and Gittleman, 1991). Yet, there are few tests of the associations between these and other species-level attributes and population change in fragmented landscapes (Haddad and Tewksbury, 2005; Ricketts, 2001).

Tropical bird communities exemplify typical responses of vertebrates to forest fragmentation (Renjifo, 1999; Sekercioglu et al., 2002). Several life history characteristics of tropical birds are thought to make them particularly sensitive to human disturbance relative to their temperate counterparts (Stratford and Robinson, 2005). Such traits include increased habitat and dietary specialization, limited dispersal ability (Laurance et al., 2004; Moore et al., 2008), and narrow physiological constraints, all of which increase home range size (Terborgh et al., 1990) and reduce population density. Tropical birds also face particularly high rates of nest predation (Newmark and Stanley, 2011; Young et al., 2008) and have slower life histories (Wiersma et al., 2007), inhibiting population

recovery (Robinson, 1999, 2001). Among tropical birds, understory insectivores and mixed-species flock participants have been shown to be most likely to decline following fragmentation (Bierregaard and Lovejoy, 1989; Stouffer and Bierregaard, 1995; Stouffer et al., 2009). Persistence of understory insectivores is influenced by fragment size and isolation (Ferraz et al., 2007; Van Houtan et al., 2007), as well as characteristics of the habitat matrix surrounding fragments (Develey and Stouffer, 2001; Gascon et al., 1999; Laurance et al., 2004; Stouffer et al., 2006). Thus, a growing literature focuses on elucidating the causes and mechanisms underlying declines of the understory insectivore guild specifically.

Much of our knowledge of the response of bird communities to human disturbance comes from a few relatively well-studied sites (e.g., Barro Colorado Island and Pipeline Road, Panama and the Biological Dynamics of Forest Fragments Project in Manaus, Brazil). Another such site is La Selva Biological Station in the lowlands of NE Costa Rica. La Selva is one of the most well-studied Neotropical forests (Gentry, 1991; McDade and Hartshorn, 1994) with avian studies dating back more than 50 years (e.g., Blake and Loiselle, 2000; Blake et al., 1990; Levey and Stiles, 1994; Slud, 1960). In 1968 when the Organization for Tropical Studies (OTS) purchased the 587 ha property from Leslie Holdridge, it was remote and surrounded by old-growth forest (McDade and Hartshorn, 1994). During the 1970s and '80s the landscape around La Selva underwent rapid deforestation. Although La Selva tripled in size by the late 1980s via acquisition of surrounding lands, it had also become isolated from other patches of lowland forest as well as the from the large, newly-protected Braulio Carrillo National Park (BCNP) at elevations above 700 m (Butterfield, 1994). Scientists raised funds for the purchase of a strip of land connecting La Selva to higher elevation forests in 1986 as part of BCNP (Stiles and Clark, 1998). Most of this corridor, as well as much of the new lands acquired by La Selva itself had been previously deforested. During the ensuing decades much of that deforested land has regrown. Areas once choked by dense exotic grasses are now closed-canopy secondary forests that, although lacking the structure and diversity of mature forest, provide habitat and improved opportunities for dispersal of forest animals (Powell et al., 2015). Concurrently, a nationwide ban on forest clearing in 1996 has slowed the rate of deforestation in northern Costa Rica from 2.2% to 1.2% per year which, in conjunction with reforestation, has led to relatively stable forest cover in the larger region (Fagan et al., 2013). Thus, from a low point in the early 1990s, it is likely that the conditions for species persistence have improved over the past two decades in and around La Selva. Consequently, if previously documented changes in La Selva's bird community result from explanations linked to area requirements or landscape connectivity, then over the past two decades, we would expect to see stability or reversals of population trends relative to earlier studies.

Research on changes in La Selva's bird community between the 1960s and the mid-1990s increased our understanding of forest bird responses to fragmentation (Sigel et al., 2010, 2006). Results from La Selva were consistent with results from other regions in that insectivores, species living in the forest understory, and species that participate in mixed-species flocks appeared to be particularly sensitive to fragmentation. However, there is no information on whether the same guilds are continuing to decline at La Selva, or whether changing land use has reversed population trends or led to different avian community changes since the 1990s. Our goals were to examine the nature of ongoing change in La Selva's avifauna in order to evaluate how recent changes in the area and connectivity of forested land in the region may have influenced the indices of bird population change. Additionally, we examined the relationships between recent population trends and species-level traits and ecological associations to refine hypotheses proposed to explain species declines and losses from tropical forest fragments generally. If previously declining groups of species continue to become rarer, such a finding would suggest that recent land acquisition and reforestation have been ineffective at mitigating declines due to either time lags or alternative drivers being more important in shaping ongoing declines. Citizen science data are used increasingly for studies of population and community change in North America (Dickinson et al., 2010), but have been rarely used in tropical regions due to lack of suitable datasets. Fortunately, Christmas Bird Counts have been conducted at La Selva since the 1980s, thus providing one of the longest-term datasets of its kind from the Neotropics. We used a consecutive 23-year data set to investigate the patterns and correlates of community change.

2. Material and methods

La Selva Biological Station (La Selva; 10°26′N, 83°59′W, 35–140 m above sea level [masl]) is located on the Caribbean slope of the Cordillera Central of Costa Rica. It is owned and operated by the OTS and consists of approximately 1611 ha of tropical wet forest (~73% old-growth forest) and disturbed habitat. Average annual precipitation is 3962 mm and mean monthly temperature ranges from 24.7 °C to 27.1 °C, consistent with a tropical wet-forest life zone (Hartshorn and Hammel, 1994; Holdridge, 1967; McDade and Hartshorn, 1994). La Selva is connected to the 44,000 ha Braulio Carrillo National Park by a 5–10 km wide corridor along its southern boundary up to ~700 masl. Above this elevation, BCNP consists primarily of old-growth forest and extends up to 3000 masl.

The Christmas Bird Count (CBC) program is the largest and oldest citizen science program in the world. CBCs began in North America in 1900 (Butcher, 1990) and at La Selva in 1985. The count occurs annually within two weeks of December 25 and consists of groups of volunteer observers identifying and counting all individual birds seen within a 24.14 km diameter area over a 24-h period. Data obtained from CBCs consist of counts of the number of individuals of each species detected, as well as information on observer effort (i.e., the number of observers, distance travelled, method of travel, and duration of each survey). CBC data have been used extensively in the analysis of population trends in N. America (e.g., Allen et al., 1995; Koenig, 2003; La Sorte and Thompson, 2007; Schmidt and Ostfeld, 2003), but to date, have not been used to evaluate the population trajectories of Neotropical birds. In the early years of CBCs at La Selva, observer effort and geographic coverage was variable, but since 1989 this count has consistently attracted a skilled group of ~30–60 observers to participate in the annual day-long survey. Because the La Selva count circle includes areas of higher-elevation forest, large rivers, farms, and towns, we restricted analyses to the nine terrestrial routes within the boundaries of the La Selva property that were surveyed consistently from 1989 to 2011. These routes covered much of the trails within the property including the CC, CCA, CCC, CCL, CES, FLA, GUA, LEP, LIA, LOC, LS, SAT, SCH, SHA, SHO, SJ, SOR, SR, SSA, SSE, SSO, STR, and SUA trails. As with any study based on data collected by citizen scientists, we caution that confounding factors that we were not able to control for may have influenced our results. However, a considerable body of research has been devoted to methods that correct for varying effort (e.g., Link and Sauer, 1999, see below). Additionally, the relatively high skill level and knowledge of the local avifauna of the La Selva observers, as well as the consistent route sampling, makes the La Selva CBC data set particularly robust. Long-term data sets from tropical regions collected under more rigorous protocols are neither available from either La Selva nor from the vast majority of Neotropical study sites.

2.1. Species-level trend models

We analyzed counts of species that are not (i) nocturnal, and thus inconsistently observed, (ii) primarily aquatic, (iii) primarily aerial foragers, and (iv) long-distance migrants as these groups do not rely exclusively on the terrestrial habitats of La Selva. We further restricted our dataset to species that met one of the following criteria: (1) detected in $\geqslant 10$ years; or (2) detected in $\geqslant 4$ of the first or last 6 years of the dataset to include extirpated species or recent colonists. Of the 520 species detected in the La Selva Christmas bird Counts between 1989 and 2011, 202 species met the criteria to be included in our analyses (Table 1). We calculated an effort adjustment parameter $H(\xi)$ in each year i to account for variation in the number of birds counted due to varying observer effort using the equation derived by Link and Sauer (1999) and Link et al. (2006):

$$H(\xi) = \frac{\left(\left(\frac{party\ hrs\ year_i}{mean\ party\ hrs} \right)^{-1.5} \right) - 1}{-1.5}$$

Because weather conditions on the count day affect bird activity, as well as the enthusiasm and ability of counters to detect birds, we included the amount of count-day rainfall as a covariate. Count-day rainfall has been shown to strongly affect count numbers at this site previously (Boyle, 2011). Daily rainfall data were collected by and obtained from the Organization for Tropical Studies (http://www.ots.ac.cr/meteoro/default.php?pestacion=2).

In our first tier of analyses, we modeled the twenty-three years of count data for each species in separate generalized linear models. We modeled counts using a Poisson distribution and a log link function. Our main explanatory variable was centred year with the effort parameter and count-day rain as covariates. Coefficients (with associated SE and P-values) for the year variable in these models represent the % change^{-yr} for each species.

2.2. Univariate correlates of population trends

We conducted a second tier of analyses exploring the univariate relationships between population trends and each of a series of variables that could provide insight into the causes of population increases or decreases: diet, habitat, flocking, body mass, and a rarity index. We built models using (i) the continuous, numerical trend coefficients, and (ii) the categorical trend classifications (increasing, decreasing, or no significant change, categorized based on P-values for the trend coefficients, above) as response variables in these univariate exploratory analyses. We investigated the relationship between diet and population trend by using two diet classifications used by the authors in different previous studies, both based on dietary descriptions from Stiles and Skutch (1989). Diet categories from Boyle (2011) were based on the predominant dietary items. Species were classified as either primarily (1) carnivorous, (2) insectivorous, (3) omnivorous, (4) frugivorous, or (5) nectarivorous. Diet categories from Sigel et al. (2006) were designed to compare strict insectivores with birds that vary their diet in one or more ways. Under this alternate classification, species were characterized as (1) carnivores (vertebrates, carrion, or vertebrates and invertebrates), (2) strict insectivores (only small invertebrates), (3) "insectivorous and other" (including arthropods and one plant-based material), (4) omnivores (a combination of more than one other category), or (5) "vegetarians" (consuming only plant material such as fruit and nectar). We also employed habitat classifications used in Sigel et al. (2006) that were based on descriptions in Stiles (1983) as follows: (1) "open" habitat species that use young second growth and open or disturbed habitats, (2) canopy/edge specialists that use only the forest canopy, (3) forest generalists that use the canopy, gaps, and/or edges and one or

more other habitats, (4) understory generalists that use the understory and one additional habitat, gaps and/or edge, and (5) understory specialists that use only the forest understory.

We grouped species according to their flocking behavior based on categorizations from Levey and Stiles (1994): (1) non-flocking species that do not participate in mixed-species flocks, (2) facultative flock members that occasionally join mixed-species flocks, or (3) nuclear flock members forming the core of mixed-species flocks. Because larger birds typically have larger home ranges, and thus, are expected to be more susceptible to local extirpation in forest fragments (Haskell et al., 2002), we tabulated mean body mass (Dunning, 1993; ln-transformed prior to analysis). Finally, we included an index of rarity based on the mean number of individuals counted early in the time frame of the study. Because species differ in their detectability, raw counts are not appropriate for estimating relative rarity (Royle et al., 2005). Thus, we ln-transformed the mean number of individuals counted for each species between 1989 and 1994, which resulted in a normal distribution of values. We then grouped species in six rarity "bins" based on values of the 10th, 25th, 50th, 75th, and 90th percentiles of this distribution with 1 being the least commonly-counted species and 6 being the most abundant species. We treated this initial rarity index as an ordinal value in our analyses. When both the dependent and independent variables were categorical, we analysed these pairwise relationships with likelihood-ratio χ^2 tests. When both dependent and independent variables were continuous, we analysed these relationships using linear regression. In all other cases where the dependent variable was continuous (i.e., population trend estimate) and the independent variable was categorical (e.g., diet, habitat) we analysed relationships with ANOVAs.

Because each trend estimate has an associated variance, we verified the univariate associations between traits and trends by employing formal meta-analytic methods that account for sample size and variance. We used the Program MetaWin (Rosenberg et al., 1999) to calculate Fisher's z-transformed effect sizes and evaluated the relationship between effect sizes and all predictor variables in a univariate context using random effects models.

2.3. Multifactorial correlates of population trends

To assess the explanatory power of our independent variables while accounting for the variation explained by other variables, we constructed general linear models using species' trend estimates as our dependent variable, and diet, habitat, flocking, ln-body mass, and rarity index as fixed, independent variables. We did not include interactions between variables because some combinations of categorical variables were missing from our dataset (e.g., none of the understory specialists were carnivores). Likewise, we were not able to use AIC model selection because most of our independent variables were categorical. However, we explored the multicollinearity among explanatory variables using a series of pairwise univariate comparisons among our predictor variables. We then used backward stepwise model selection to eliminate variables explaining little variation in population trends of the species in our dataset with cut-offs to leave the model of $P = 0.2$.

Due to the special interest in understory insectivores and our inability to consider interactions between habitat and diet explicitly, we separately analysed trends of insectivores only, comparing those living in the understory relative to those living in other habitat types. We then restricted analyses to only understory birds, comparing insectivores to other dietary guilds. To do this, we combined data for both understory generalists and specialists and compared (i) the insectivore population trends to those of other dietary guilds, and (ii) insectivores in understory habitats to insectivores inhabiting other habitat types. We conducted all analyses in JMP (SAS Institute Inc., 2009). The complete dataset including trend

Table 1

Species included in this study with trend estimates, associated SE, likelihood-ratio χ^2 values, P-values, and mean number of individuals counted over all years of the study. All models df = 3. Trends significant at $P \leqslant 0.05$ are in bold font.

Scientific name	Common name	% change^{-yr}	SE (%)	L-R χ^2	P	Mean count
Tinamus major	**Great Tinamou**	**3.25**	**0.65**	**25.3**	**<.0001**	**37.9**
Crypturellus soui	**Little Tinamou**	**−3.00**	**1.33**	**5.2**	**0.0232**	**9.0**
Crypturellus boucardi	**Slaty-breasted Tinamou**	**−3.77**	**1.03**	**13.4**	**0.0002**	**15.0**
Ortalis cinereiceps	**Gray-headed Chachalaca**	**−7.50**	**1.54**	**25.1**	**<.0001**	**7.5**
Penelope purpurascens	**Crested Guan**	**7.32**	**0.89**	**68.8**	**<.0001**	**23.2**
Crax rubra	Great Curassow	3.31	1.98	2.8	0.0935	4.1
Mesembrinibis cayennensis	**Green Ibis**	**10.80**	**1.65**	**45.5**	**<.0001**	**7.0**
Coragyps atratus	Black Vulture	−0.56	0.56	1.0	0.3200	49.2
Sarcoramphus papa	King Vulture	2.86	2.27	1.6	0.2073	3.1
Leptodon cayanensis	**Gray-headed Kite**	**11.60**	**2.89**	**17.8**	**<.0001**	**2.4**
Harpagus bidentatus	Double-toothed Kite	0.89	2.61	0.1	0.7330	2.3
Accipiter superciliosus	Tiny Hawk	6.44	5.75	1.3	0.2569	0.5
Leucopternis semiplumbeus	Semiplumbeous Hawk	2.81	1.68	2.8	0.0952	5.7
Buteo nitidus	Gray Hawk	−0.83	4.45	0.0	0.8520	1.1
Micrastur ruficollis	**Barred Forest-Falcon**	**−32.04**	**12.01**	**12.8**	**0.0003**	**0.3**
Micrastur mirandollei	Slaty-backed Forest-Falcon	−4.21	3.41	1.6	0.2126	1.4
Micrastur semitorquatus	**Collared Forest-Falcon**	**−7.09**	**3.11**	**5.4**	**0.0199**	**1.7**
Herpetotheres cachinnans	Laughing Falcon	3.33	1.98	2.8	0.0934	4.7
Falco rufigularis	Bat Falcon	−6.10	4.73	1.7	0.1872	0.9
Laterallus albigularis	**White-throated Crake**	**−5.44**	**1.67**	**10.9**	**0.0009**	**6.0**
Aramides cajaneus	**Gray-necked Wood-Rail**	**6.84**	**2.66**	**6.9**	**0.0085**	**2.4**
Patagioenas cayennensis	Pale-vented Pigeon	3.44	1.93	3.2	0.0753	4.4
Patagioenas speciosa	**Scaled Pigeon**	**−19.70**	**3.50**	**34.7**	**<.0001**	**2.4**
Patagioenas flavirostris	Red-billed Pigeon	2.23	1.62	1.9	0.1698	6.0
Patagioenas nigrirostris	**Short-billed Pigeon**	**−1.57**	**0.57**	**7.5**	**0.0061**	**47.3**
Columbina talpacoti	**Ruddy Ground-Dove**	**6.68**	**2.59**	**6.9**	**0.0087**	**2.5**
Claravis pretiosa	Blue Ground-Dove	−5.67	3.11	3.5	0.0627	1.9
Leptotila verreauxi	White-tipped Dove	0.42	4.11	0.0	0.9192	0.9
Leptotila cassini	**Gray-chested Dove**	**−2.97**	**1.16**	**6.6**	**0.0102**	**11.8**
Geotrygon veraguensis	Olive-backed Quail-Dove	2.15	1.60	1.8	0.1783	6.1
Geotrygon montana	Ruddy Quail-Dove	3.84	3.99	0.9	0.3348	1.0
Aratinga finschi	**Crimson-fronted Parakeet**	**−2.95**	**1.19**	**6.2**	**0.0126**	**11.6**
Aratinga nana	Olive-throated Parakeet	−0.04	0.60	0.0	0.9432	44.7
Ara ambiguus	**Great Green Macaw**	**13.95**	**1.36**	**111.2**	**<.0001**	**14.5**
Brotogeris jugularis	**Orange-chinned Parakeet**	**4.75**	**0.60**	**63.6**	**<.0001**	**46.0**
Pyrilia haematotis	Brown-hooded Parrot	−0.73	0.57	1.7	0.1968	49.0
Pionus senilis	**White-crowned Parrot**	**1.06**	**0.52**	**4.1**	**0.0422**	**57.7**
Amazona autumnalis	**Red-lored Parrot**	**7.05**	**0.54**	**179.0**	**<.0001**	**58.1**
Amazona farinosa	Mealy Parrot	−0.65	0.37	3.1	0.0797	113.4
Piaya cayana	**Squirrel Cuckoo**	**2.30**	**0.73**	**10.0**	**0.0016**	**29.4**
Crotophaga sulcirostris	Groove-billed Ani	0.61	1.41	0.2	0.6663	8.0
Glaucis aeneus	**Bronzy Hermit**	**−5.76**	**2.04**	**8.2**	**0.0043**	**3.8**
Threnetes ruckeri	Band-tailed Barbthroat	0.83	2.51	0.1	0.7417	2.6
Phaethornis longirostris	Long-billled Hermit	0.66	0.62	1.1	0.2913	40.9
Phaethornis striigularis	**Stripe-throated Hermit**	**4.38**	**0.78**	**31.8**	**<.0001**	**27.0**
Eutoxeres aquila	**White-tipped Sicklebill**	**23.65**	**9.33**	**9.5**	**0.0021**	**0.4**
Florisuga mellivora	**White-necked Jacobin**	**−7.93**	**3.02**	**7.3**	**0.0069**	**2.0**
Klais guimeti	**Violet-headed Hummingbird**	**−6.74**	**2.21**	**9.7**	**0.0019**	**3.4**
Thalurania colombica	Violet-crowned Woodnymph	−0.86	1.33	0.4	0.5183	8.8
Amazilia amabilis	Blue-chested Hummingbird	−5.81	3.00	3.8	0.0507	2.3
Amazilia tzacatl	**Rufous-tailed Hummingbird**	**−2.54**	**0.83**	**9.4**	**0.0022**	**22.8**
Chalybura urochrysia	**Bronze-tailed Plumeleteer**	**−7.27**	**1.72**	**18.8**	**<.0001**	**5.9**
Heliothryx barroti	Purple-crowned Fairy	−1.39	2.09	0.4	0.5056	3.7
Trogon clathratus	**Lattice-tailed Trogon**	**−8.31**	**2.95**	**8.4**	**0.0038**	**1.9**
Trogon massena	**Slaty-tailed Trogon**	**4.63**	**0.78**	**35.9**	**<.0001**	**27.0**
Trogon violaceus	Violaceous Trogon	−1.38	1.19	1.3	0.2464	11.1
Trogon rufus	**Black-throated Trogon**	**3.43**	**0.77**	**20.2**	**<.0001**	**27.6**
Baryphthengus martii	**Rufous Motmot**	**3.96**	**0.93**	**18.4**	**<.0001**	**18.3**
Electron platyrhynchum	**Broad-billed Motmot**	**3.47**	**0.70**	**25.1**	**<.0001**	**33.0**
Notharchus hyperrhynchus	**White-necked Puffbird**	**10.94**	**2.46**	**20.5**	**<.0001**	**3.5**
Notharchus tectus	Pied Puffbird	5.30	4.30	1.5	0.2188	1.1
Malacoptila panamensis	White-whiskered Puffbird	6.23	2.98	4.5	0.0334	1.9
Monasa morphoeus	**White-fronted Nunbird**	**−17.06**	**2.31**	**69.3**	**<.0001**	**5.1**
Galbula ruficauda	Rufous-tailed Jacamar	2.15	1.48	2.1	0.1453	7.3
Jacamerops aureus	**Great Jacamar**	**−42.90**	**21.91**	**8.5**	**0.0035**	**0.2**
Pteroglossus torquatus	**Collared Aracari**	**4.86**	**0.52**	**90.4**	**<.0001**	**60.9**
Ramphastos sulfuratus	**Keel-billed Toucan**	**3.06**	**0.53**	**32.9**	**<.0001**	**55.5**
Ramphastos swainsonii	**Chestnut-mandibled Toucan**	**2.69**	**0.48**	**31.5**	**<.0001**	**68.7**
Melanerpes pucherani	**Black-cheeked Woodpecker**	**3.91**	**0.74**	**28.3**	**<.0001**	**29.3**
Picoides fumigatus	Smoky-brown Woodpecker	1.69	4.83	0.1	0.7269	0.9
Piculus simplex	**Rufous-winged Woodpecker**	**5.27**	**1.83**	**8.5**	**0.0036**	**4.9**
Celeus loricatus	**Cinnamon Woodpecker**	**10.31**	**2.54**	**18.2**	**<.0001**	**2.9**
Celeus castaneus	Chestnut-colored Woodpecker	0.21	2.10	0.0	0.9192	3.6

Table 1 (continued)

Scientific name	Common name	% change^{-yr}	SE (%)	L-R χ^2	P	Mean count
Dryocopus lineatus	Lineated Woodpecker	1.81	1.79	1.0	0.3127	4.9
Campephilus guatemalensis	**Pale-billed Woodpecker**	**3.17**	**0.80**	**15.7**	**<.0001**	**25.0**
Cymbilaimus lineatus	**Fasciated Antshrike**	**9.11**	**1.77**	**28.2**	**<.0001**	**5.8**
Taraba major	**Great Antshrike**	**−7.49**	**2.32**	**11.0**	**0.0009**	**3.3**
Thamnophilus doliatus	**Barred Antshrike**	**5.92**	**2.36**	**6.3**	**0.0122**	**3.3**
Thamnophilus atrinucha	**Western Slaty-Antshrike**	**10.31**	**0.97**	**118.4**	**<.0001**	**21.9**
Dysithamnus striaticeps	Streak-crowned Antvireo	−3.45	2.47	2.0	0.1600	3.4
Myrmotherula axillaris	**White-flanked Antwren**	**−4.82**	**2.37**	**4.2**	**0.0396**	**2.9**
Myrmotherula fulviventris	Checker-throated Antwren	−4.87	2.91	2.9	0.0868	2.3
Microrhopias quixensis	**Dot-winged Antwren**	**−9.50**	**2.66**	**13.8**	**0.0002**	**2.6**
Cercomacra tyrannina	Dusky Antbird	1.87	1.49	1.6	0.2085	7.0
Myrmeciza exsul	Chestnut-backed Antbird	0.53	0.66	0.7	0.4174	37.0
Hylophylax naevioides	Spotted Antbird	−1.41	2.57	0.3	0.5811	2.5
Gymnopithys leucaspis	Bicolored Antbird	−3.92	2.06	3.7	0.0551	3.7
Phaenostictus mcleannani	**Ocellated Antbird**	**4.58**	**1.58**	**8.5**	**0.0035**	**6.4**
Hylopezus perspicillatus	Streak-chested Antpitta	1.40	5.04	0.1	0.7817	0.7
Hylopezus dives	**Thicket Antpitta**	**−8.30**	**3.29**	**6.8**	**0.0090**	**1.7**
Formicarius analis	**Black-faced Antthrush**	**−9.40**	**1.17**	**69.7**	**<.0001**	**13.2**
Synallaxis brachyura	**Slaty Spinetail**	**−11.92**	**3.42**	**13.9**	**0.0002**	**1.8**
Automolus ochrolaemus	**Buff-throated Foliage-gleaner**	**−8.50**	**2.80**	**9.9**	**0.0017**	**2.3**
Xenops minutus	Plain Xenops	0.77	1.68	0.2	0.6472	5.6
Dendrocincla fuliginosa	Plain-brown Woodcreeper	0.61	1.70	0.1	0.7184	5.3
Glyphorynchus spirurus	Wedge-billed Woodcreeper	0.38	0.59	0.4	0.5204	45.6
Dendrocolaptes sanctithomae	**Northern Barred Woodcreeper**	**3.19**	**0.97**	**10.8**	**0.0010**	**17.0**
Xiphorhynchus susurrans	**Cocoa Woodcreeper**	**7.74**	**1.27**	**38.4**	**<.0001**	**11.1**
Xiphorhynchus lachrymosus	Black-striped Woodcreeper	0.15	1.92	0.0	0.9388	4.1
Xiphorhynchus erythropygius	Spotted Woodcreeper	−3.45	3.97	0.8	0.3817	1.0
Lepidocolaptes souleyetii	**Streak-headed Woodcreeper**	**4.73**	**1.25**	**14.5**	**0.0001**	**10.4**
Ornithion brunneicapillus	Brown-capped Tyrannulet	0.76	2.21	0.1	0.7324	3.2
Capsiempis flaveola	**Yellow Tyrannulet**	**−9.27**	**1.79**	**29.2**	**<.0001**	**5.9**
Elaenia flavogaster	Yellow-bellied Elaenia	0.39	1.92	0.0	0.8379	4.3
Mionectes olivaceus	Olive-striped Flycatcher	−1.71	2.67	0.4	0.5203	2.7
Mionectes oleagineus	Ochre-bellied Flycatcher	0.82	1.06	0.6	0.4390	13.9
Zimmerius vilissimus	Paltry Tyrannulet	−1.28	0.95	1.8	0.1784	17.0
Myiornis atricapillus	**Black-capped Pygmy-Tyrant**	**3.40**	**0.86**	**15.5**	**<.0001**	**22.6**
Oncostoma cinereigulare	Northern Bentbill	−2.42	1.90	1.6	0.2017	4.3
Poecilotriccus sylvia	Slate-headed Tody-Flycatcher	4.83	4.60	1.1	0.2913	0.8
Todirostrum cinereum	Common Tody-Flycatcher	0.76	1.27	0.4	0.5520	9.8
Todirostrum nigriceps	Black-headed Tody-Flycatcher	−1.70	2.27	0.6	0.4524	3.1
Rhynchocyclus brevirostris	**Eye-ringed Flatbill**	**−10.11**	**3.73**	**8.0**	**0.0046**	**1.3**
Tolmomyias sulphurescens	Yellow-olive Flycatcher	1.27	2.55	0.2	0.6191	3.5
Tolmomyias assimilis	Yellow-margined Flycatcher	2.50	1.73	2.1	0.1482	5.2
Platyrinchus coronatus	Golden-crowned Spadebill	−5.35	3.63	2.2	0.1351	1.3
Terenotriccus erythrurus	Ruddy-tailed Flycatcher	−3.52	2.60	1.9	0.1729	2.4
Contopus cinereus	Tropical Pewee	0.12	2.47	0.0	0.9605	2.6
Colonia colonus	Long-tailed Tyrant	1.52	1.60	0.9	0.3421	6.1
Attila spadiceus	**Bright-rumped Atilla**	**4.37**	**0.86**	**26.3**	**<.0001**	**22.3**
Rhytipterna holerythra	**Rufous Mourner**	**4.66**	**0.98**	**23.0**	**<.0001**	**17.2**
Myiarchus tuberculifer	**Dusky-capped Flycatcher**	**4.48**	**1.18**	**14.5**	**0.0001**	**12.0**
Pitangus sulphuratus	**Great Kiskadee**	**3.83**	**0.75**	**26.3**	**<.0001**	**28.5**
Megarhynchus pitangua	**Boat-billed Flycatcher**	**4.64**	**0.69**	**46.6**	**<.0001**	**34.8**
Myiozetetes similis	**Social Flycatcher**	**−1.89**	**0.63**	**9.0**	**0.0027**	**40.0**
Myiozetetes granadensis	Gray-capped Flycatcher	−0.41	0.71	0.3	0.5684	31.6
Conopias albovittatus	White-ringed Flycatcher	−0.56	1.16	0.2	0.6332	11.5
Tyrannus melancholicus	**Tropical Kingbird**	**4.08**	**0.89**	**21.1**	**<.0001**	**20.1**
Tityra semifasciata	**Masked Tityra**	**4.07**	**0.72**	**32.6**	**<.0001**	**31.6**
Tityra inquisitor	**Black-crowned Tityra**	**8.04**	**1.60**	**26.0**	**<.0001**	**6.8**
Pachyramphus cinnamomeus	Cinnamon Becard	0.90	1.08	0.7	0.402	14.0
Pachyramphus polychopterus	White-winged Becard	−3.39	2.61	1.7	0.1910	2.4
Querula purpurata	Purple-throated Fruitcrow	−1.66	1.12	2.2	0.1382	12.5
Cephalopterus glabricollis	Bare-necked Umbrellabird	−2.41	2.02	1.4	0.2322	3.8
Lipaugus unirufus	**Rufous Piha**	**−5.64**	**1.12**	**26.2**	**<.0001**	**13.0**
Carpodectes nitidus	Snowy Cotinga	3.34	1.77	3.6	0.0579	5.1
Manacus candei	White-collared Manakin	−0.24	0.56	0.2	0.6602	50.6
Corapipo altera	White-ruffed Manakin	0.80	1.53	0.3	0.5988	6.7
Ceratopipra mentalis	**Red-capped Manakin**	**−6.97**	**0.93**	**58.7**	**<.0001**	**19.4**
Hylophilus ochraceiceps	Tawny-crowned Greenlet	−2.93	3.37	0.8	0.3819	1.4
Hylophilus decurtatus	**Lesser Greenlet**	**5.59**	**0.62**	**83.5**	**<.0001**	**43.5**
Vireolanius pulchellus	**Green Shrike-Vireo**	**5.15**	**2.60**	**4.1**	**0.0441**	**2.4**
Cyanocorax morio	**Brown Jay**	**−17.00**	**2.66**	**52.1**	**<.0001**	**3.9**
Campylorhynchus zonatus	**Band-backed Wren**	**3.40**	**1.28**	**7.2**	**0.0073**	**9.8**
Pheugopedius atrogularis	Black-throated Wren	0.99	1.38	0.5	0.4694	8.2
Cantorchilus nigricapillis	Bay Wren	−1.29	0.70	3.5	0.0629	32.5
Cantorchilus thoracicus	**Stripe-breasted Wren**	**5.86**	**0.88**	**45.5**	**<.0001**	**21.4**
Cantorchilus modestus	**Plain Wren**	**−5.78**	**2.03**	**8.5**	**0.0036**	**4.3**

Table 1 (continued)

Scientific name	Common name	% change^{-yr}	SE (%)	L-R χ^2	P	Mean count
Troglodytes aedon	House Wren	0.57	1.75	0.1	0.7440	5.2
Henicorhina leucosticta	White-breasted Wood-Wren	−0.15	0.46	0.1	0.7501	72.6
Microcerculus philomela	**Nightingale Wren**	**−13.28**	**2.94**	**23.8**	**<.0001**	**2.5**
Cyphorhinus phaeocephalus	**Song Wren**	**−8.00**	**3.41**	**5.9**	**0.0153**	**1.6**
Microbates cinereiventris	Tawny-faced Gnatwren	−0.81	3.81	0.0	0.8304	1.1
Ramphocaenus melanurus	**Long-billed Gnatwren**	**8.07**	**1.83**	**19.7**	**<.0001**	**6.2**
Polioptila plumbea	Tropical Gnatcatcher	1.75	0.90	3.8	0.0520	19.3
Turdus obsoletus	Pale-vented Thrush	−1.27	0.85	2.2	0.1340	22.0
Turdus grayi	**Clay-colored Thrush**	**3.45**	**0.62**	**31.0**	**<.0001**	**41.4**
Geothlypis poliocephala	Gray-crowned Yellowthroat	5.22	4.75	1.2	0.2659	1.5
Geothlypis semiflava	Olive-crowned Yellowthroat	−5.47	3.42	2.6	0.1038	0.7
Phaeothlypis fulvicauda	**Buff-rumped Warbler**	**8.75**	**0.96**	**86.7**	**<.0001**	**18.8**
Coereba flaveola	Bananaquit	−1.69	1.37	1.5	0.2165	8.4
Mitrospingus cassinii	**Dusky-faced Tanager**	**2.86**	**0.95**	**9.2**	**0.0025**	**17.9**
Tachyphonus luctuosus	White-shouldered Tanager	−0.74	1.10	0.4	0.5038	13.4
Tachyphonus delatrii	**Tawny-crested Tanager**	**−15.31**	**3.74**	**20.6**	**<.0001**	**1.8**
Tachyphonus rufus	White-lined Tanager	−2.61	2.63	1.0	0.3178	2.7
Ramphocelus sanguinolentus	Crimson-collared Tanager	1.55	2.34	0.4	0.5093	2.8
Ramphocelus passerinii	Passerini's Tanager	0.32	0.47	0.4	0.5063	70.8
Thraupis episcopus	**Blue-gray Tanager**	**6.20**	**0.82**	**58.0**	**<.0001**	**25.1**
Thraupis palmarum	**Palm Tanager**	**2.91**	**0.83**	**12.3**	**0.0004**	**23.3**
Tangara larvata	Golden-hooded Tanager	0.05	0.64	0.0	0.9355	39.0
Tangara inornata	Plain-colored Tanager	3.62	1.53	5.7	0.0173	6.9
Tangara gyrola	Bay-headed Tanager	5.33	3.73	2.0	0.1523	2.1
Tangara icterocephala	**Silver-throated Tanager**	**7.41**	**0.98**	**58.1**	**<.0001**	**17.5**
Dacnis venusta	Scarlet-thighed Dacnis	0.53	1.23	0.2	0.6677	11.8
Dacnis cayana	Blue Dacnis	1.70	1.14	2.2	0.1381	12.2
Chlorophanes spiza	**Green Honeycreeper**	**6.89**	**1.20**	**33.8**	**<.0001**	**12.0**
Cyanerpes lucidus	Shining Honeycreeper	0.02	1.11	0.0	0.9845	13.5
Cyanerpes cyaneus	Red-legged Honeycreeper	1.35	1.89	0.5	0.4768	6.3
Saltator coerulescens	Grayish Saltator	−15.71	4.34	14.0	0.0002	1.4
Saltator maximus	Buff-throated Saltator	−1.01	0.74	1.9	0.1733	29.0
Saltator atriceps	**Black-headed Saltator**	**−7.09**	**1.39**	**27.5**	**<.0001**	**9.1**
Saltator grossus	**Slate-colored Grosbeak**	**−7.95**	**2.02**	**16.4**	**<.0001**	**4.2**
Volatina jacarina	**Blue-black Grassquit**	**−10.88**	**1.76**	**42.7**	**<.0001**	**7.3**
Sporophila americana	**Variable Seedeater**	**1.88**	**0.90**	**4.4**	**0.0362**	**19.7**
Oryzoborus funereus	**Thick-billed Seed-Finch**	**−16.80**	**3.53**	**27.1**	**<.0001**	**1.9**
Arremon aurantiirostris	Orange-billed Sparrow	−1.37	0.76	3.3	0.0699	27.7
Arremonops conirostris	**Black-striped Sparrow**	**−6.36**	**1.85**	**12.3**	**0.0004**	**5.6**
Habia fuscicauda	Red-throated Ant-Tanager	0.24	0.84	0.1	0.7771	23.2
Chlorothraupis carmioli	**Carmiol's Tanager**	**−9.86**	**4.62**	**5.0**	**0.0252**	**0.9**
Caryothraustes poliogaster	Black-faced Grosbeak	−0.30	0.86	0.1	0.7248	21.2
Cyanocompsa cyanoides	Blue-black Grosbeak	−1.60	1.77	0.8	0.3649	5.0
Quiscalus mexicanus	Great-tailed Grackle	0.89	1.78	0.3	0.6163	6.5
Molothrus aeneus	**Bronzed Cowbird**	**56.94**	**4.11**	**695.5**	**<.0001**	**12.1**
Icterus prosthemelas	**Black-cowled Oriole**	**6.21**	**1.92**	**10.7**	**0.0011**	**4.6**
Icterus mesomelas	Yellow-tailed Oriole	−7.56	4.49	3.0	0.0818	1.0
Amblycercus holosericeus	**Yellow-billed Cacique**	**−7.10**	**2.32**	**9.8**	**0.0017**	**3.3**
Cacicus uropygialis	**Scarlet-rumped Cacique**	**1.05**	**0.53**	**4.0**	**0.0447**	**55.4**
Psarocolius wagleri	**Chestnut-headed Oropendola**	**8.73**	**0.63**	**196.9**	**<.0001**	**44.7**
Psarocolius montezuma	**Montezuma Oropendola**	**2.83**	**0.31**	**83.7**	**<.0001**	**164.9**
Euphonia luteicapilla	**Yellow-crowned Euphonia**	**3.08**	**0.82**	**14.1**	**0.0002**	**23.7**
Euphonia gouldi	**Olive-backed Euphonia**	**1.84**	**0.44**	**17.7**	**<.0001**	**81.9**
Euphonia minuta	**White-vented Euphonia**	**−14.83**	**2.92**	**30.7**	**<.0001**	**2.7**

results and ecological classifications for all species is archived at Dryad (http://dx.doi.org/10.1016/j.biocon.2015.01.004). Scientific and common names follow the American Ornithologists' Union (1998) and all updates to that list current to Oct 2013 (Chesser et al., 2013).

3. Results

3.1. What are the population trends of La Selva's resident terrestrial avifauna?

Of the 202 species we analyzed, over half (107 species, 53%) showed evidence of a directional change. Although more species increased (63) than decreased (44), the absolute rate of change was greater in declining species than in increasing species (ln-transformed rates, $t_{105} = -3.5$, $P < 0.005$). Species that declined significantly were declining on average at $-9.9\%^{-yr}$ (±0.9%) and species with significant increasing trends were only increasing on average at $6.5\%^{-yr}$ (±0.7%). Trend estimates of eight increasing species exceeded $10\%^{-yr}$: Bronzed Cowbird (*Molothrus aeneus*, 56.9%), White-tipped Sicklebill (*Eutoxeres aquila*, 23.6%), Great Green Macaw (*Ara ambiguus*, 13.9%), Grey-headed Kite (*Leptodon cayanensis*, 11.6%), White-necked Puffbird (*Notharchus hyperrhynchus*, 10.9%), Green Ibis (*Mesembrinibis cayennensis*, 10.8%), Western Slaty-Antshrike (*Thamnophilus atrinucha*, 10.3%), and Cinnamon Woodpecker (*Celeus loricatus*, 10.3%). Five species were not counted during the last six years of data we analyzed, apparently becoming extirpated from La Selva during this time; Great Jacamar (*Jacamerops aureus*), Barred Forest-Falcon (*Micrastur ruficollis*), Tawny-crested Tanager (*Tachyphonus delatrii*), Thick-billed Seed-Finch (*Oryzoborus funereus*), and Carmiol's Tanager (*Chlorothraupis*

carmioli). Trend estimates of eight additional decreasing species exceeded $-10\%^{-yr}$: Scaled Pigeon (*Patagioenas speciosa*, -19.7%), White-fronted Nunbird (*Monasa morphoeus*, -17.1%), Brown Jay (*Cyanocorax morio*, -17.0%), Grayish Saltator (*Saltator coerulescens*, -15.7%), White-vented Euphonia (*Euphonia minuta*, -14.8%), Nightingale Wren (*Microcerculus philomela*, -13.3%), Slaty Spinetail (*Synallaxis brachyura*, -11.9%), Blue–black Grassquit (*Volatina jacarina*, -10.9%), and Eye-ringed Flatbill (*Rhynchocyclus brevirostris*, -10.1%).

3.2. Univariate associations between ecological factors and ongoing change

Population trends did not differ among dietary groups using either the classification of Sigel et al. (2006; $F_{4,193} = 0.6$, $P = 0.681$; Fig. 1A) or the classification of Boyle (2011; $F_{4,193} = 0.8$, $P = 0.508$; Fig. 1B). By contrast, when we grouped species based on whether their population trends were decreasing, no change, or increasing, these groups differed in dietary attributes when we used the classifications of Boyle (2011; likelihood ratio $\chi^2 = 18.9$, df = 8, $P = 0.015$; Fig. S1), and were suggestive of a difference when we used the diet classifications of Sigel et al. (2006; likelihood ratio $\chi^2 = 14.5$, df = 8, $P = 0.071$; Fig. S2). Contrary to expectation, we found no evidence that insectivores were faring worse than other guilds under either classification. Most (53.3%) insectivores showed no clear directional trend with 18.2% increasing and 28.6% decreasing. Nectarivores appeared to be experiencing the most negative population trends with 38.5% of species experiencing significant declines compared to 16.7–26.2% of species declining in other guilds (Fig. 1).

Habitat use was strongly associated with population trends in analyses of both continuous ($F_{4,193} = 4.4$, $P = 0.002$; Fig. S3A) and categorical response variables (likelihood ratio $\chi^2 = 19.1$, df = 8, $P = 0.014$; Fig. S3B). Canopy and edge species had the most positive population trends ($2.0\%^{-yr} \pm 1.6\%^{-yr}$ SE) whereas birds inhabiting open areas and understory specialists had the most negative population trends ($-2.1\%^{-yr} \pm 0.9\%^{-yr}$ SE and $-2.4\%^{-yr} \pm 1.7\%^{-yr}$ SE, respectively).

Flocking behavior was not associated with either continuous metrics ($F_{2,190} = 2.2$, $P = 0.114$; Fig. S4A) or categorical metrics (likelihood ratio $\chi^2 = 1.6$, df = 4, $P = 0.816$; Fig. S4B) of population trends. However, trends in the data are consistent with previous findings that mixed-species flock participants are particularly vulnerable (e.g., Sigel et al., 2010, 2006); mean population trends for nuclear flocking species were negative and 95% CI did not overlap 0 ($2.7\%^{-yr} \pm 1.2\%^{-yr}$ SE).

The univariate relationship between body mass and our continuous metric of population trend was non-significant, but tended to be weakly positive (% change$^{-yr} = -2.2 + 0.537*ln$-mass, $F_{1,200} = 1.8$, $P = 0.185$; Fig. S5A). We found suggestive evidence of a difference in mean body mass among species with increasing, decreasing, or unchanging population trends ($F_{2,199} = 2.9$, $P = 0.057$; Fig. S5B) with increasing species being on average 61.2 g (±1.2 g) and decreasing species being on average 40.5 g (±1.2 g).

Rarity index was not related to continuous metrics of population trend ($F_{5,196} = 0.7$, $P = 0.616$; Fig. S6A). However, rarity index varied among species with increasing, decreasing, and unchanging population trends (likelihood ratio $\chi^2 = 19.3$, df = 10, $P = 0.037$; Fig. S6B). Increasing species were more common in the early years of CBCs at La Selva than species with unchanging or negative population trends.

The meta-analytic approach resulted in similar results as those using raw trends. Trends in effect sizes related to variation in diet, flocking, mass, and initial rarity mirrored those using raw trend data but were not statistically significant at $\alpha = 0.05$. Variation in
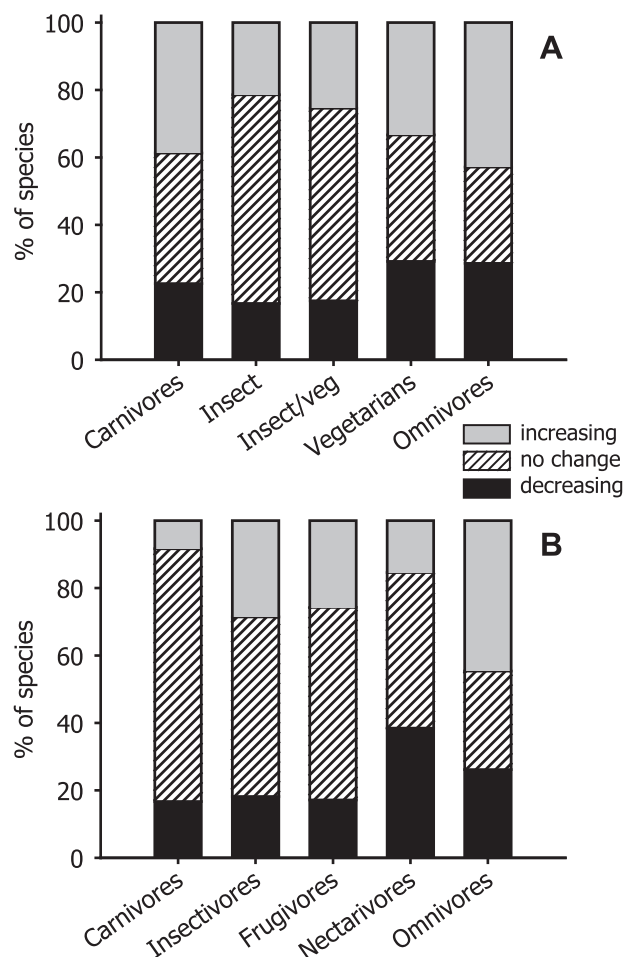

Fig. 1. Analyses of the relationships between diet and population change reveal that insectivores are not any more likely to be declining than other dietary groups in analyses based on diet classifications taken from either Sigel et al. (2006; panel A) or classifications taken from Boyle (2011; panel B). The relationship between diet classifications and the% of species increasing (grey bars), decreasing (black bars), or not showing evidence of directional change (hatched bars) is sensitive to classification scheme, even when those classifications are based on the same source material (Stiles and Skutch, 1989). Panel A depicts suggestive evidence for carnivorous and omnivorous guilds to be over-represented among the increasing species and vegetarian and omnivorous to be weakly over-represented among declining species (likelihood ratio $\chi^2 = 14.5$, df = 8 $P = 0.071$). In contrast, panel B suggests nectarivores are strongly over-represented among the declining species, whereas carnivores are under-represented among the increasing species (likelihood ratio $\chi^2 = 18.9$, df = 8 $P = 0.015$).

effect size was associated with habitat, with species using open areas declining most strongly and forest generalists increasing most strongly ($Q_{5,196} = 0.9$, $P = 0.002$).

3.3. Multifactorial associations between ecological factors and ongoing change

Our initial multifactorial model including all predictor variables (diet, habitat, flocking, *ln*-mass, and rarity index) explained much of the variation in population trend in our dataset ($F_{16,181} = 2.1$, $P = 0.009$). However, pairwise analyses of our predictor variables indicated strong collinearity among several variables (Table 2; Supplementary Figs. S1–S6): diet covaried with habitat (Fig. S7), body mass (Fig. S9), and rarity (Fig. S10); habitat covaried with flocking (Fig. S11) and rarity (Fig. S13); and flocking covaried with body mass (Fig. S14). Backwards variable selection resulted in a final model including only habitat and body mass ($R^2 = 0.11$,

Table 2
Pairwise associations between predictor variables potentially associated with population trends. Associations between pairs of categorical (i.e., diet, habitat, and flocking) and/or ordinal (i.e., rarity bins) variables are based on likelihood ratio χ^2 tests; associations between the continuous variable (i.e., ln-body mass) and categorical variables are based on ANOVAs. Supplementary Figs. S7–S16 depict these relationships graphically.

	Habitat	Flocking	Body Mass	Rarity
Diet	$\chi^2 = 37.5$, df = 16, $P = 0.002$	$\chi^2 = 13.3$, df = 8, $P = 0.102$	$F_{4,197} = 44.8$, $P < 0.0001$	$\chi^2 = 60.8$, df = 20, $P < 0.0001$
Habitat		$\chi^2 = 24.4$, df = 8, $P = 0.002$	$F_{4,197} = 2.3$, $P = 0.063$	$\chi^2 = 35.6$, df = 20, $P = 0.017$
Flocking			$F_{2,190} = 8.6$, $P < 0.001$	$\chi^2 = 6.2$, df = 10, $P = 0.795$
Body mass				$F_{5,196} = 1.5$, $P = 0.189$
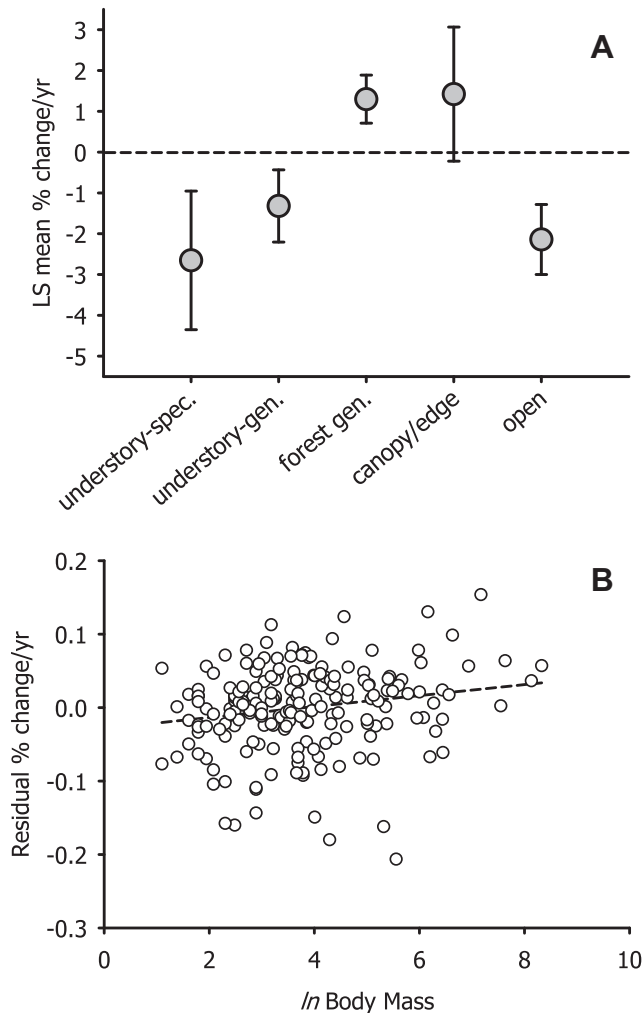
Fig. 2. Least square mean trend estimates (±SE) for birds of different habitat associations (after accounting for variation due to body mass; panel A) and the relationship between ln-body mass and the residuals of a habitat-only model (panel B). These two factors were the only two included in a final model to explain population trends using backwards stepwise variable selection (see Sections 2.3 and 3.3).

$F_{5,192} = 4.6$, $P < 0.001$). We explored a range of P-values to enter and leave the model; all values from 0.2 to 0.05 resulted in the same final model. Population trends were most negative in species inhabiting either the understory or highly disturbed open areas ($F_{4,192} = 4.1$, $P = 0.004$; Fig. 2A) and species having small body size (effect test ln-mass, $F_{1,192} = 5.4$, $P = 0.022$; Fig. 2B). After accounting for variation in trends associated with habitat, a ln-1 g increase in body mass was associated with a $0.66\%^{-yr}$ more positive trend coefficient.

In analyses specifically aimed at elucidating the population trajectories of understory insectivores, we found little evidence that among understory birds, insectivores were faring worse than other dietary guilds (one tailed t-test, $t_{50} = 1.0$, $P = 0.169$; Fig. 3A). Consistent with analyses of the whole community, we found a strong relationship between habitat and population trends in the insectivore guild; like other dietary guilds, insectivorous species living in the understory had more negative population trends than did insectivores living in other habitats (one tailed t-test, $t_{74} = -3.0$, $P = 0.004$; Fig. 3B). Thus, understory living was associated with population declines, but insectivores, whether they live in the understory or elsewhere, did not appear to respond differently than other dietary guilds.

4. Discussion

The avifauna of La Selva Biological Station is highly dynamic, with more than half the species that we analyzed significantly increasing or decreasing. Over the past two decades, population increases have occurred among initially common species and forest generalists, but the declining species have changed more rapidly. Among the species that increased or decreased rapidly, we found little pattern with respect to size, taxonomy, or any of the ecological and behavioral traits we examined. Consistent with previous studies at La Selva (Sigel et al., 2010, 2006) and elsewhere in the tropics (Robinson, 1999; Stouffer et al., 2009), we found that birds dependent on the forest understory continue to decline, which could possibly reflect lag effects in population change following landuse change. As would be expected by ongoing land use change and forest regrowth, we also found that birds dependent on degraded non-forest habitats are, on average, the species with the most rapid population declines. However, contrary to the findings of previous studies at La Selva (Sigel et al., 2010, 2006), we found no evidence that population trends of insectivores are more negative than other dietary guilds. Additionally, after accounting for the strong habitat effects, we found that small-bodied species are faring worse than larger species. These results suggest a re-evaluation of the causes of ongoing community change in this, and possibly other tropical forest sites.

Although diet was associated with population change in univariate analyses, our results were not consistent with prior studies. Regardless of the diet classification scheme, insectivores were not more likely to be declining than other guilds. Indeed, results based on the classification specifically designed to examine the vulnerability of specialized insectivores (i.e., that of Sigel et al., 2006) revealed even less association between diet and population trend than results based on the alternate classification scheme. These conclusions were verified by analyses in which we restricted the dataset to understory birds, and compared insectivores against all other dietary guilds.

Our failure to find evidence of insectivores being particularly vulnerable contrasts with an emerging paradigm in tropical avian ecology (e.g., this special issue). We consider four potential explanations. First, it is possible that susceptible insectivores are the first to be extirpated and had already declined to densities too low to be included in our analyses prior to the time frame of our study. If true, this hypothesis predicts that the foraging niches of
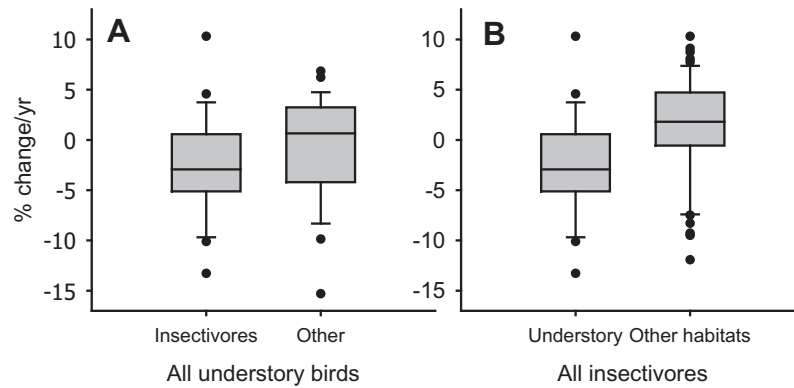
Fig. 3. Box plots depicting trend estimates for insectivores inhabiting understory habitats vs. all other habitats (panel A), and all understory birds contrasting those that primarily consume insects vs. species of other dietary guilds.

extirpated insectivores may differ systematically from those that apparently are stable. Any test of foraging differences could provide insight into the mechanisms underlying divergent population trends. While many insectivore species had declined at La Selva prior to the initiation of this study, 73 species of this guild remain common enough to be included in our analysis, providing ample opportunity for more narrowly-focused experimental and observational studies to test this hypothesis. A related second hypothesis is that the causes of decline over previous time periods differ from the causes of ongoing declines. Deforestation and fragmentation are but two of the anthropogenic pressures experienced by Neotropical birds. The relative importance of alternate factors may have shifted over the previous half century. Our finding of strong declines in species requiring non-forest habitats highlights this possibility, given the regrowth into secondary forest of much of the formerly open areas of La Selva during this study. This result contrasts starkly with the fact that only two decades ago, not a single bird dependent on such habitats was declining (Levey and Stiles, 1994). Similar declines and extirpations of non-forest species occurred at BCI as forest regenerated and open habitats disappeared (Robinson, 1999, 2001; Sigel et al., 2010). Unfortunately, neither of these first two hypotheses could be tested directly in the context of this study. However, we encourage other researchers to consider temporal shifts in the causes and patterns of decline when designing future studies.

A third alternative explanation for our failure to find predicted relationships between population trends and understory insectivorous guilds is that many previous studies did not control for variation in body size, and diet may have been confounded with body size. Indeed, we found a very strong relationship between dietary guild and body size (Fig. S9), and this relationship likely explains the declining population trends of nectarivores, as most nectarivores in our study were small-bodied (e.g., hummingbirds). Likewise, carnivores were represented by relatively few declining species (Fig. 1A), and this dietary guild was associated with large body size (Fig. S9). To test the possibility that declines in nectar resources or changes plant-hummingbird interactions drove the declines in small-bodied species, we re-ran our set of multi-factorial models excluding the nectarivore guild. These analyses resulted in the same two variables retained in our final model (habitat and ln-mass; $F_{5,180} = 4.2$, $P = 0.001$). The effect size for body mass was similar in the restricted dataset relative to the model based on the full dataset ($0.62\%^{-yr}_{restricted}$ vs. $0.66\%^{-yr}_{full}$ for a ln-1 g increase in body mass; $F_{1,180} = 4.2$, $P = 0.049$). These results strengthen the evidence that body size is a strong driver of population decline that operates independent of diet.

The joint associations of habitat and body size with population trends may well provide crucial insight into the drivers of current population change at La Selva. Body size is associated with impor-

tant physiological, ecological, and life history traits that may underlie population change. A review of global extinction risk in birds found that extinction risk from habitat loss was prevalent among birds with smaller body size, whereas larger-bodied species were more susceptible to human persecution (Owens and Bennett, 2000). At La Selva, where direct human persecution on large-bodied species is minimized by anti-poaching measures, we may be witnessing only one aspect of this general pattern. However, the proposed link between habitat loss and body size results from unspecified forms of specialization (Owens and Bennett, 2000), which presumably increases home range size and reduces population density—an argument that essentially boils down to area requirements. Do small-bodied species, irrespective of dietary guild, exhibit consistently greater specialization with consequences for density and demographic rates? It is possible, but extremely hard to evaluate empirically due to the challenges of identifying and measuring all important axes of niche breadth. Dispersal distance is a more tractable alternative link between body size and demographic rates, and studies are accruing that provide valuable data on typical dispersal distances and dispersal limitation for Neotropical birds (Burney and Brumfield, 2009; Moore et al., 2008; Tarwater, 2012; Woltmann et al., 2012).

A new and unexplored alternative hypothesis for the patterns presented here is that declines of small Neotropical birds are driven by physiological responses to climatic stressors. Small birds have high metabolic rates that require higher and more constant food intake rates (Calder, 1974). Small birds also pay greater thermoregulatory costs when temperatures are either too low or too high (Gardner et al., 2011; McKechnie and Wolf, 2010). If changes in forest productivity (Clark et al., 2003, 2010) are resulting in trophic-wide reductions in food, such changes in food abundance would likely affect the small birds first. Likewise, increases in mean or extreme temperatures will prove more challenging for small birds than larger ones, particularly when accompanied by high humidity (Gerson et al., 2014; Powers, 1992). Understory birds may be acutely susceptible to such climatic changes as the understory is a place of little diurnal and seasonal fluctuation in temperature and humidity relative to the canopy and other exposed habitats (Stratford and Robinson, 2005; although results of Pollock et al. (2015) are not consistent with this hypothesis). Consistent with climate and physiological processes driving population changes, species such as the Tawny-Crested Tanager (*Tachyphonus delatrii*) and Carmiol's Tanager (*Chlorothraupis carmioli*) that had declined dramatically by the mid-1990s and now have apparently disappeared from La Selva, remain common in mixed-species flocks at higher elevation locally (W.A. Boyle, unpublished data).

We acknowledge that multiple drivers may be leading to the highly dynamic nature of this community. The hypotheses pro-

posed to explain population declines of Neotropical birds are nearly as diverse as the communities they seek to explain. This is confounded by collinearity among ecological predictor variables, as revealed in our pairwise analyses (Table 2; Figs. S7–16), which makes it difficult to isolate ecological factors associated with avian community changes. Nevertheless, clarifying the correlates of ongoing change is an important exercise as it focuses attention on the most plausible factors given current patterns of change. Some proposed hypotheses such as insecticide drift from nearby industrial agricultural operations would disproportionately affect insectivores, and could not easily explain the habitat or body size patterns. Likewise, arguments hinging on dietary specialization, although potentially useful for explaining past changes in La Selva's avifauna, are also of limited value for explaining the current trajectories of this community. The continuing decline of understory birds may be attributable, in part, to indirect effects of altered climates or changes in mesoherbivore populations on plant community structure and prey availability for understory birds (Michel and Sherry, 2012), although any potential relationship between shifts in understory prey and vegetation structure and body size requires further investigation. We propose that the next steps involve testing predictions capable of determining whether the underlying drivers of population declines result from factors that effectively reduce population size and limit colonization, or whether those declines result from factors having more direct and immediate effects on individual fitness. Well-designed experimental tests will be especially valuable if they can disentangle the causative relationships driving individual-level and population-level processes that scale up to shape communities of tropical birds around the world.

5. Conclusions

The results of this study provide evidence of an avifauna in flux. Although some of the news is good news, we are far from understanding why, after decades of study, many of the bird species of La Selva continue to disappear. Our results suggest that future studies should pay close attention to possible body size effects when examining associations between species-level traits and population declines. In particular, direct tests are needed of physiologically-based hypotheses consistent with both the habitat associations and the size dependency of declining species. Our work highlights the immense worth of long-term datasets from diverse tropical locales where multiple stressors, including fragmentation and climate change, are leading to the extirpation and extinction of an untold fraction of the earth's biodiversity.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.01.004.

References

Allen, C.R., Lutz, R.S., Demarais, S., 1995. Red imported fire ant impacts on Northern Bobwhite populations. Ecol. Appl. 5, 632–638.

American Ornithologists' Union, 1998. Checklist of North American Birds, seventh ed. American Ornithologists' Union, Washington, DC.

Bierregaard, R.O., Lovejoy, T.E., 1989. Effects of forest fragmentation on Amazonian understory bird communities. Acta Amazonica 19, 215–241.

Blake, J.G., Loiselle, B.A., 2000. Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. Auk 117, 663–686.

Blake, J.G., Stiles, F.G., Loiselle, B.A., 1990. Birds of La Selva Biological Station: habitat use, trophic composition, and migrants. In: Gentry, A. (Ed.), Four Neotropical Rainforests. Yale University Press, New Haven, pp. 161–182.

Boyle, W.A., 2011. Short-distance partial migration of Neotropical birds: a community-level test of the foraging limitation hypothesis. Oikos 120, 1803–1816.

Burney, C.W., Brumfield, R.T., 2009. Ecology predicts levels of genetic differentiation in Neotropical birds. Am. Nat. 174, 358–368.

Butcher, G.S., 1990. Audubon Christmas Bird Counts, In Survey designs and statistical methods for the estimation of avian population trends. In: Sauer, J.R., Droege, S. (Ed.). U.S. Fish and Wildlife Service, Biological Report, vol. 90(1).

Butterfield, R.P., 1994. The regional context: land colonization and conservation in La Selva. In: McDade, L.A., Bawa, K.S., Hespenheide, H.A., Hartshorn, G.S. (Eds.), La Selva: Ecology and Natural History of a Neotropical Rain Forest. The University of Chicago Press, Chicago, IL, pp. 299–306.

Calder, W.A., 1974. Consequences of body size for avian energetics. In: Paynter, R.A. (Ed.), Avian Energetics, vol. 15. Nuttall Ornithological Club Publication, Cambridge, MA, pp. 86–144.

Chesser, R.K., Banks, R.C., Barker, F.K., Cicero, C., Dunn, J.L., Kratter, A.W., Lovette, I.J., Rasmussen, P.C., Remsen, J.V., Rising, J.D., Stotz, D.F., Winker, K., 2013. Fifty-fourth supplement to the American Ornithologists' Union *Check-list of North American Birds*. Auk 130, 558–571.

Clark, D.A., Piper, S.C., Keeling, C.D., Clark, D.B., 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. Proc. Nation. Acad. Sci. United States of America 100, 5852–5857.

Clark, D.B., Clark, D.A., Oberbauer, S.F., 2010. Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO_2. Glob. Change Biol. 16, 747–759.

Develey, P.F., Stouffer, P.C., 2001. Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. Conserv. Biol. 15, 1416–1422.

Dickinson, J.L., Zuckerberg, B., Bonter, D.N., 2010. Citizen science as an ecological research tool: challenges and benefits. In: Futuyma, D.J., Shafer, H.B., Simberloff, D. (Eds.), Annual Review of Ecology, Evolution, and Systematics, vol. 41, pp. 149–172.

Dirzo, R., Raven, P.H., 2003. Global state of biodiversity and loss. Annu. Rev. Environ. Resour. 28, 137–167.

Dunning, J.B., 1993. Avian Body Masses. CRC Press, Boca Raton, FL.

Fagan, M.E., DeFries, R.S., Sesnie, S.E., Arroyo, J.P., Walker, W., Soto, C., Chazdon, R.L., Sanchun, A., 2013. Land cover dynamics following a deforestation ban in northern Costa Rica. Environ. Res. Lett. 8, 034017.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Ann. Rev. Ecol. Evol. Syst. 34, 487–515.

Ferraz, G., Nichols, J.D., Hines, J.E., Stouffer, P.C., Bierregaard, R.O., Lovejoy, T.E., 2007. A large-scale deforestation experiment: effects of patch area and isolation on Amazon birds. Science 315, 238–241.

Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L., Heinsohn, R., 2011. Declining body size: a third universal response to warming? Trends Ecol. Evol. 26, 285–291.

Gascon, C., Lovejoy, T.E., Bierregaard, R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M., Borges, S., 1999. Matrix habitat and species richness in tropical forest remnants. Biol. Conserv. 91, 223–229.

Gentry, A.H. (Ed.), 1991. Four Neotropical Rainforests. Yale University Press, New Haven, CT.

Gerson, A.R., Krabbe Smith, E., Smit, B., McKechnie, A.E., Wolf, B.O., 2014. The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. Physiol. Biochem. Zool. 87 (published online Nov 2014).

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381.

Gompper, M.E., Gittleman, J.L., 1991. Home range scaling: intraspecific and comparative trends. Oecologia 87, 343–348.

Haddad, N.M., Tewksbury, J.J., 2005. Low-quality habitat corridors as movement conduits for two butterfly species. Ecol. Appl. 15, 250–257.

Hartshorn, G.S., Hammel, B.E., 1994. Vegetation types and floristic patterns. In: McDade, L.A., Bawa, K.S., Hespenheide, H.A., hartshorn, G.S. (Eds.), In La Selva: Ecology and Natural History of a Neotropical Rain Forest. The University of Chicago Press, Chicago, IL, pp. 73–89.

Haskell, J.P., Ritchie, M.E., Olff, H., 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. Nature 418, 527–530.

Holdridge, L.R., 1967. Life Zone Ecology. Tropical Science Center, San José, Costa Rica.

Koenig, W.D., 2003. European Starlings and their effect on native cavity-nesting birds. Conserv. Biol. 17, 1134–1140.

La Sorte, F.A., Thompson, F.R., 2007. Poleward shifts in winter ranges of North American birds. Ecology 88, 1803–1812.

Laurance, W.F., 2008. Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. Biol. Conserv. 141, 1731–1744.

Laurance, S.G.W., Stouffer, P.C., Laurance, W.E., 2004. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. Conserv. Biol. 18, 1099–1109.

Levey, D.J., Stiles, G.F., 1994. Birds: ecology, behavior, and taxonomic affinities. In: McDade, L.A., Bawa, K.S., Hespenheide, H.A., Hartshorn, G.S. (Eds.), La Selva: ecology and natural history of a neotropical rain forest. The University of Chicago Press, Chicago, pp. 217–228.

Link, W.A., Sauer, J.R., 1999. Controlling for varying effort in count surveys: an analysis of Christmas Bird Count data. J. Agri., Biol., Environ. Stat. 4, 116–125.

Link, W.A., Sauer, J.R., Niven, D.K., 2006. Heirarchial model for regional analysis of population change using Christmas Bird Count data, with application to the American Black Duck. The Condor 108, 13–24.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

McDade, L.A., Hartshorn, G.S., 1994. La Selva Biological Station. In: McDade, L.A., Bawa, K.S., Hespenheide, H.A., hartshorn, G.S. (Eds.), In La Selva: Ecology and Natural History of a Neotropical Rain Forest. The University of Chicago Press, Chicago, IL, pp. 6–14.

McKechnie, A.E., Wolf, B.O., 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. Biol. Lett. 6, 253–256.

Michel, N.L., Sherry, T.W., 2012. Human-altered mesoherbivore densities and cascading effects on plant and animal communities in fragmented tropical forests. In: Sudarshana, P. (Ed.), In Tropical Forests, InTech.

Moore, R.P., Robinson, W.D., Lovette, I.J., Robinson, T.R., 2008. Experimental evidence for extreme dispersal limitation in tropical forest birds. Ecol. Lett. 11, 960–968.

Newmark, W.D., Stanley, T.R., 2011. Habitat fragmentation reduces nest survival in an Afrotropical bird community in a biodiversity hotspot. Proc. Nation. Acad. Sci. United States of America 108, 11488–11493.

Owens, I.P.F., Bennett, P.M., 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proc. Nation. Acad. Sci. 97, 12144–12148.

Pollock, H.S., Cheviron, Z.A., Brawn, J.D., 2015. Absence of microclimate selectivity in insectivorous birds of the Neotropical forest understory. Biol. Conserv. 188, 116–125.

Powell, L.L., Wolfe, J.D., Johnson, E.I., Hines, J.E., Nichols, J.D., Stouffer, P.C., When is secondary Amazonian forest "recovered" in terms of habitat transition probabilities? A case study using radio-tagged insectivorous understory birds. Biological Conservation.

Powers, D.R., 1992. Effect of temperature and humidity on evaporative water loss in Anna's hummingbird (*Caypte anna*). J. Comparative Physiol. B-Biochem. Syst. Environ. Physiol. 162, 74–84.

Renjifo, L.M., 1999. Composition changes in a subandean avifauna after long-term forest fragmentation. Conserv. Biol. 13, 1124–1139.

Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. Am. Nat. 158, 87–99.

Robinson, W.D., 1999. Long-term changes in the avifauna of Barro Colorado Island, Panama, a tropical forest isolate. Conserv. Biol. 13, 85–97.

Robinson, W.D., 2001. Changes in abundance of birds in a Neotropical forest fragment over 25 years: a review. Animal Biodiver. Conserv. 24, 51–65.

Rosenberg, M.S., Adams, D.C., Gurevich, J., 1999. MetaWin: Statistical Software for Meta-Analysis. Sinauer Associates, Sunderland, Massachusetts.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge.

Royle, J.A., Nichols, J.D., Kery, M., 2005. Modelling occurrence and abundance of species when detection is imperfect. Oikos 110, 353–359.

SAS Institute Inc., 2009. JMP, Version 8.0.2, Cary, NC.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conserv. Biol. 5, 18–32.

Schmidt, K.A., Ostfeld, R.S., 2003. Songbird populations in fluctuating environments: predator responses to pulsed resources. Ecology 84, 406–415.

Sekercioglu, C.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D., Sandi, R.F., 2002. Disappearance of insectivorous birds from tropical forest fragments. Proc. Nation. Acad. Sci., USA 99, 263–267.

Sigel, B.J., Sherry, T.W., Young, B.E., 2006. Avian community response to lowland tropical rainforest isolation: 40 years of change at La Selva Biological Station, Costa Rica. Conserv. Biol. 20, 111–121.

Sigel, B.J., Robinson, W.D., Sherry, T.W., 2010. Comparing bird community responses to forest fragmentation in two lowland Central American reserves. Biol. Conserv. 143, 340–350.

Slud, P., 1960. The birds of finca "La Selva", Costa Rica: a tropical wet forest locality. Bull. Am. Museum Nat. History 121, 49–148.

Stiles, F.G., 1983. Checklist of Birds. In: Janzen, D.H. (Ed.), Costa Rican Natural History. University of Chicago Press, Chicago, IL, pp. 530–544.

Stiles, G.F., Clark, D.A., 1998. Conservation of tropical rain forest birds: a case study from Costa Rica American Birds 43, 420–428.

Stiles, F.G., Skutch, A.F., 1989. A Field Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, NY.

Stouffer, P.C., Bierregaard, R.O., 1995. Use of Amazonian forest fragments by understory insectivorous birds. Ecology 76, 2429–2445.

Stouffer, P.C., Bierregaard, R.O., Strong, C., Lovejoy, T.E., 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. Conserv. Biol. 20, 1212–1223.

Stouffer, P.C., Strong, C., Naka, L.N., 2009. Twenty years of understorey bird extinctions from Amazonian rain forest fragments: consistent trends and landscape-mediated dynamics. Diver. Distrib. 15, 88–97.

Stratford, J.A., Robinson, W.D., 2005. Gulliver travels to the fragmented tropics: geographic variation in mechanisms of avian extinction. Front. Ecol. Environ. 3, 91–98.

Tarwater, C.E., 2012. Influence of phenotypic and social traits on dispersal in a family living, tropical bird. Behavior. Ecol. 23, 1242–1249.

Terborgh, J., Robinson, S.K., Parker III, T.A., Munn, C.A., Pierpont, N., 1990. Structure and organization of an Amazonian forest bird community. Ecol. Monogr. 60, 213–238.

Turner, I.M., 1996. Species loss in fragments of tropical rain forest: a review of the evidence. J. Appl. Ecol. 33, 200–209.

Van Houtan, K.S., Pimm, S.L., Halley, J.M., Bierregaard Jr., R.O., Lovejoy, T.E., 2007. Dispersal of Amazonian birds in continuous and fragmented forest. Ecol. Lett. 10, 219–229.

Wiersma, P., Muñoz-Garcia, A., Walker, A., Williams, J.B., 2007. Tropical birds have a slow pace of life. Proc. Nation. Acad. Sci., USA 104, 9340–9345.

Woltmann, S., Sherry, T.W., Kreiser, B.R., 2012. A genetic approach to estimating natal dispersal distances and self-recruitment in resident rainforest birds. J. Avian Biol. 43, 33–42.

Young, B.E., Sherry, T.W., Sigel, B.J., Woltmann, S., 2008. Nesting success of Costa Rican lowland rain forest birds in response to edge and isolation effects. Biotropica 40, 615–622.