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## Testing the microclimate hypothesis: Light environment and population trends of Neotropical birds

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### ABSTRACT

Species vary in their vulnerability to extirpation or extinction in response to habitat loss, including deforestation. A variety of correlates of vulnerability have been found, but few empirical data have been gathered that provide insight into potential causation. We attempted to elucidate cause via a test of the “microclimate hypothesis” at two sites in the northern Neotropics. We censused birds at 234 points that varied in distance from a deforested edge to >2 km into a forest. At each of these points we recorded or calculated ten environmental and microclimate variables that allowed us to tie environmental data to bird assemblages directly. We found that canopy cover increased, wind decreased, and ambient temperature, vapor pressure density, and heat index varied little or not at all with distance from a forested edge. Yet light penetration was the key variable, as the light environment was affected within 50 m of an edge, and many species were associated with low-light conditions. Crucially, on the basis of regional population trends, species in low-light environments are more vulnerable to extirpation. Our results provide the clearest support to date of the hypothesis that sensitivity to light is a key factor limiting occupancy of birds in fragmented tropical forests and lend support to at least this aspect of the microclimate hypothesis.

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### 1. Introduction

Studies of Neotropical forests have documented numerous edge effects (Laurance et al., 2002) and have shown that species loss is non-random in the wake of deforestation or habitat loss and alteration (e.g., Patten et al., 2010; Sigel et al., 2010). A wide variety of correlates of extinction risk for various organisms have been found, including those based on life history, ecological, and phylogenetic traits (Didham et al., 1998; Carvalho and Vasconcelos, 1999; Brown and Hutchings, 1997; Fisher and Owens, 2004; Sodhi et al., 2004; Bennett et al., 2005; Stratford and Robinson, 2005; Gray et al., 2007; Lindell et al., 2007; Patten and Smith-Patten, 2009, 2011). For birds these traits have included body size (Roff and Roff, 2003; Gage et al., 2004; Gaston, 2006), geographic range size (Cardillo et al., 2008; Harris and Pimm, 2008), limited dispersal ability (Moore et al., 2008; Lees and Peres, 2009; Ibarra-Macias et al., 2011), as well as life span, disturbance of redox homeostasis, tendency to congregate, and foraging behavior in terms of both a species' foraging stratum and dietary guild (Gray et al., 2007; Constantini, 2008; Lees and Peres, 2008; Reif et al., 2010; Patten and Smith-Patten, 2011). Some correlates come with a caution to pay

heed to spatial scale (Pearman, 2002; Patten and Smith-Patten, 2011); nonetheless, given the breadth of research conducted within different habitats and patch sizes, and on a variety of plants, invertebrates, and vertebrates, a strong foundation has been built correlating edge effects and species' traits with extinction risk.

But, elucidating underlying mechanisms—moving along the gradient from correlation toward causation of extirpation—was the goal of our study. We wished to move beyond effects attributed solely to “distance from edge,” which, like latitude, is a proxy for environmental variables (e.g., Patten, 2004; Qian et al., 2009) but is not in itself a cause of extirpation or population declines. Hence, our specific goal was to identify potential environmental variables, in this case microclimate, slight changes in climate at different strata and at varying distances within habitat. Microclimate has been suggested as a factor in explaining edge effects and species declines (Sekercioglu et al., 2002; Stratford and Robinson, 2005), but empirical studies have been largely descriptive (e.g., Evens, 1939; Ashton, 1958), botanical (Young and Mitchell, 1994; Davies-Colley et al., 2000), or indirectly tied to animals (Canaday, 1997; Stevens and Husband, 1998; Pearman, 2002). Directly tying a suite of microclimatic measurements to assemblage data and population trends for animals has yet to be done.

We conducted such a study at two Central American forests, one a lowland, semi-moist forest, the other a wet foothill forest. We censused bird assemblages throughout these forests and

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directly tied those assemblages to microclimate where they were recorded. We reasoned that if there is an underlying mechanism of vulnerability to changes in specific microclimate variables, then the effects of microclimate would hold within different forests that have similar birds, thereby validating the assumption, along the lines of the “microclimate hypothesis,” that tropical birds are constrained physiologically to the putatively cool, moist, calm, and dark of a forest’s interior. Even more important for conservation is being able to relate species’ population trends to environmental and physiological constraints, which we were able to do in this study.

### 1.1. Testing the “microclimate hypothesis”

We were interested in both how microclimate varies with distance from a forest edge and at what point a threshold is reached. The latter, to use Harper et al.’s (2005:771) terminology, refers to the “distance of edge influence” (DI), defined as “the set of distances from the edge into the adjacent community over which there is a statistically significant EI [=edge influence],” itself defined as the abiotic and biotic processes “that result in a detectable difference in composition, structure, or function near the edge, as compared with the ecosystem on either side of the edge.” Various ecologists have measured how environmental variables change with distance into tropical and temperate forests from a deforested edge (e.g., Williams-Linera, 1990; Matlack, 1993; Didham and Lawton, 1999; Davies-Colley et al., 2000; Gehlhausen et al., 2000; Newmark, 2001). Among microclimate variables measured, most studies have reported that light penetration and wind speed increased sharply near an edge, whereas ambient temperature and relative humidity (or other air moisture metrics) tended to change less abruptly (Kapos, 1989; Williams-Linera, 1990; Matlack, 1993; Gehlhausen et al., 2000; Newmark, 2001). The shape of the relationship between edge influence and distance from an edge is not necessarily linear (Malcolm, 1994; Young and Mitchell, 1994; Camargo and Kapos, 1995; Murcia, 1995; Chen et al., 1999; Newmark, 2001); instead, a given variable, such as light penetration, may decline sharply a short distance into a forest away from an edge and thereafter flatten, or the relationship may be curvilinear. Shape aside, DI tends to be within 100 m of a forest edge (Murcia, 1995; Laurance, 2004; Harper et al., 2005), especially in tropical ecosystems.

Coupled with these advances in our understanding of how microclimates vary with respect to habitat edges and fragmentation has been an increased understanding of how habitat occupancy by a species or guild is shaped by microclimate (Bestelmeyer, 2000 [ants]; Van Wilgenburg et al., 2001 [arthropods]; Pearman, 2002 [birds]; Prinzing, 2005 [arthropods]). Together these lines of evidence might be viewed as *prima facie* support for what Sekercioglu et al. (2002:263) dubbed the “microclimate hypothesis,” the idea—following Karr and Freemark’s (1983), Turner’s (1996), and Canaday’s (1997) leads—that tropical forest birds “are particularly sensitive physiologically to changes in microclimate associated with forest fragmentation.”

Yet there has been little in the way of direct tests of the “microclimate hypothesis” (Stratford and Robinson, 2005). We moved toward a direct test by first looking at the basis of the hypothesis—how microclimate grades throughout a tropical forest—and then generating attendant predictions of how microclimate may constrain avian assemblages within specific microclimates. We began with the idea, on the basis of prior research, that the forest interior is a cool, moist, calm, and dark haven for true forest bird species. We then predicted that we would be able to tie ambient temperature, air moisture, wind speed, and light penetration directly to particular avian species. We further predicted that one climatic variable would have such a strong correlation to an assemblage’s presence and to known population trends that it would

point toward a physiological constraint keeping certain species within specific microclimates.

## 2. Methods

### 2.1. Study sites

We collected data at 234 points at two study sites in the northern Neotropics—La Milpa Field Station, Orange Walk, Belize (~17.8°N, 89°W), a lowland, semi-moist forest with elevations <150 m ( $n = 130$  points; 8–10 January, 5–8 June, 25–30 December 2010, and 26–30 April 2011) and Las Cruces Biological Station, Puntarenas, Costa Rica (~8.8°N, 83.0°W), a wet foothill forest at 1100–1300 m elevation ( $n = 104$  points; 13–16 June 2010 and 7–10 May 2011). La Milpa lies within the Rio Bravo Conservation and Management Area, a vast (~105,200 ha) protected area managed by Programme for Belize. Cleared farmland, as close as 3.5 km from the field station, surrounds the northern portion of Rio Bravo, but the main portion of the reserve abuts the Gallon Jug private reserve of ~54,154 ha, which is primarily still forested, as well as parks and reserves in neighboring Guatemala. Las Cruces, managed by the Organization for Tropical Studies, protects a much smaller (~300 ha) remnant patch of forest surrounded by pastures and rural dwellings.

### 2.2. Field methods

We censused birds using 10-min. point counts that we conducted throughout the day, weather permitting (not overly hot or windy or having more than light rain; conditions that can hinder bird activity or detectability). Individual birds heard or seen within a fixed radius of 25 m were counted (always by Patten). We selected points haphazardly along roads, trails, and footpaths at varying distances from an edge throughout the forest, with points having a minimum of 50 m between them during a given survey period. To minimize pseudoreplication, we paid particular attention to any birds that could be recounted, by vocalization or movement, at our next point. For instance, if a bird surveyed previously moved in the same direction we headed, then we would not proceed with another count until we were sure that bird had departed, as we felt it better to undercount a species than to double count an individual. No points were surveyed along the same reach of trail during the same survey period.

In this study an edge refers to any deforested, mowed, or similarly disturbed area or clearing with a width of  $\geq 10$  m and a discontinuous canopy; examples included the field station compounds, lumber camps, wide roads, and pastures. We estimated distance to an edge while in the field, but our “distance from edge” metric was verified or altered by plotting a point’s latitude–longitude (determined with a Garmin®etrex Vista HCx Global Positioning System unit) onto satellite maps in Google Earth 6 and using that software to calculate a linear distance to the nearest edge. We ground-truthed a subset of data-collection points and some landmarks that are clearly visible on Google Earth to reduce measurement error. We conducted surveys anywhere from an edge itself to as far as 2629 m into a forest from the nearest anthropogenic edge.

We recorded environmental data, five environmental and five microclimate variables, at each point count. The environmental data included ambient wind (Beaufort scale), cloud cover (% of clouds overhead), rainfall (either none or light, as point counts were only conducted when there was no or light rain), distance to nearest edge (m), and canopy cover (%). Percent canopy cover was determined using a manual GRS densitometer, which allows one to get a percentage of cover based on the meter’s grid.

We recorded four microclimate variables in the field—ambient temperature (°C), relative humidity (%), heat index (°C), wind speed (m/s)—at the ground and 2 m above the ground. These variables were measured using a hand-held Kestrel®4500 Pocket Weather Tracker. We let the meter stabilize, usually 10–15 min. for the first reading of the day and ~5 min. thereafter, before recording measurements. We used ambient temperature and relative humidity to calculate (from formulae in Lawrence 2005) dew point, saturation vapor pressure, and actual vapor pressure. Our measure of humidity was vapor pressure deficit (VPD), defined as saturation minus actual vapor pressure, in hectorPascals (hPa). We transformed our field variables into VPD because it is considered to have more biological meaning than simply relating organisms to relative humidity (Anderson 1936). Our fifth microclimate variable, light intensity (kLux), was measured using an Extech®EasyView EA30 digital light meter placed on the ground. Because light intensity tends to fluctuate rapidly in tropical forests, we recorded a minimum and maximum value at each point.

### 2.3. Data analysis

We excluded all boreal migrants because our interests were in the resident tropical species. We also excluded all canopy (crown) species; i.e., only species that occur typically between the subcanopy and the ground were retained for analyses. As a means of assessing potential spatial autocorrelation in the avian assemblage between adjacent points, for each such pair of points we calculated both a linear distance (using a spherical law of cosines formula) and a quantitative Sørensen's index of dissimilarity. We reasoned that if there was spatial autocorrelation, then dissimilarity between points separated by 100 m would be significantly lower than dissimilarity between points separated by >100 m. We used a two-sample *t*-test against the null hypotheses that mean dissimilarity did not differ between points <100 m and >100 m apart.

We used only the microclimate values taken at 2 m above ground, following Chen et al. (1999). As mentioned above, microclimate measures tended to be stable at a given point with the exception of light. We calculated both a median value and a range to assess light penetration. We expected our microclimate variables to vary with time of day in addition to with distance from a forest edge. As a result, we removed the time-of-day effect by retaining residuals from quadratic regressions of the variable regressed against time and used these residuals as our response variables in all subsequent analyses. To assess how a microclimate variable was associated with distance from edge, we regressed the residual of the variable against  $\log_{10}$  distance, although to approximate DI we ran a two-segment piecewise regression with the same variables and treated the breakpoint as the DI.

We associated bird species with microclimate in two ways. First, we conducted a canonical correspondence analysis (CCA) separately for La Milpa and Las Cruces data. For these analyses we discarded any species not recorded on at least three points at a given site, which in addition to our elimination of canopy species (see Fig. 3 for species included in analyses), reduced our number of points by one for each study site. Like other ordination techniques in the correspondence analysis family, CCA uses the raw data of richness and abundance to plot both sample points and species in multivariate space (the ordination of species was our primary interest). CCA differs in being a direct technique that constrains the ordination by a multiple regression of the environmental (microclimate) variables provided a priori. Because environmental variables are incorporated into the analysis, a two-dimensional graph of, say, species along the first two ordination axes also may include a biplot of the direction and relative influence of each environmental variable. This aspect of CCA renders it a direct ordination, in contrast to the indirect ordinations that require a post

hoc association to environmental variables. We further examined the relationship between distance from a forested edge and light penetration by plotting difference scores between points on which the species was recorded and points it was not.

Our final goal was to associate microclimate to population trend. Avian population trends have not been published for either La Milpa or Las Cruces; nevertheless, data are available for sites that lie in the same biogeographic regions (*sensu* Patten and Smith-Patten, 2008). For La Milpa, data are occupancy trends from Palenque, Chiapas, Mexico (Patten et al., 2010; Patten and Smith-Patten, 2011), a regional site that has virtually the same bird assemblage (pers. obs.). For Las Cruces, data are from qualitative statements—sharp increase, modest increase, stable, modest decrease, sharp decrease, or extirpated—about trends at Barro Colorado Island (BCI), Panama, and La Selva Biological Station, Costa Rica (Robinson, 2001; Sigel et al., 2010), sites that bracket Las Cruces, which is more-or-less midway between them. For species recorded at both BCI and La Selva, we used the qualitative score presented by those sources that suggested the most pressing conservation concern, e.g., we scored *Attila spadiceus* as “modest decrease” (BCI) rather than “stable” (La Selva).

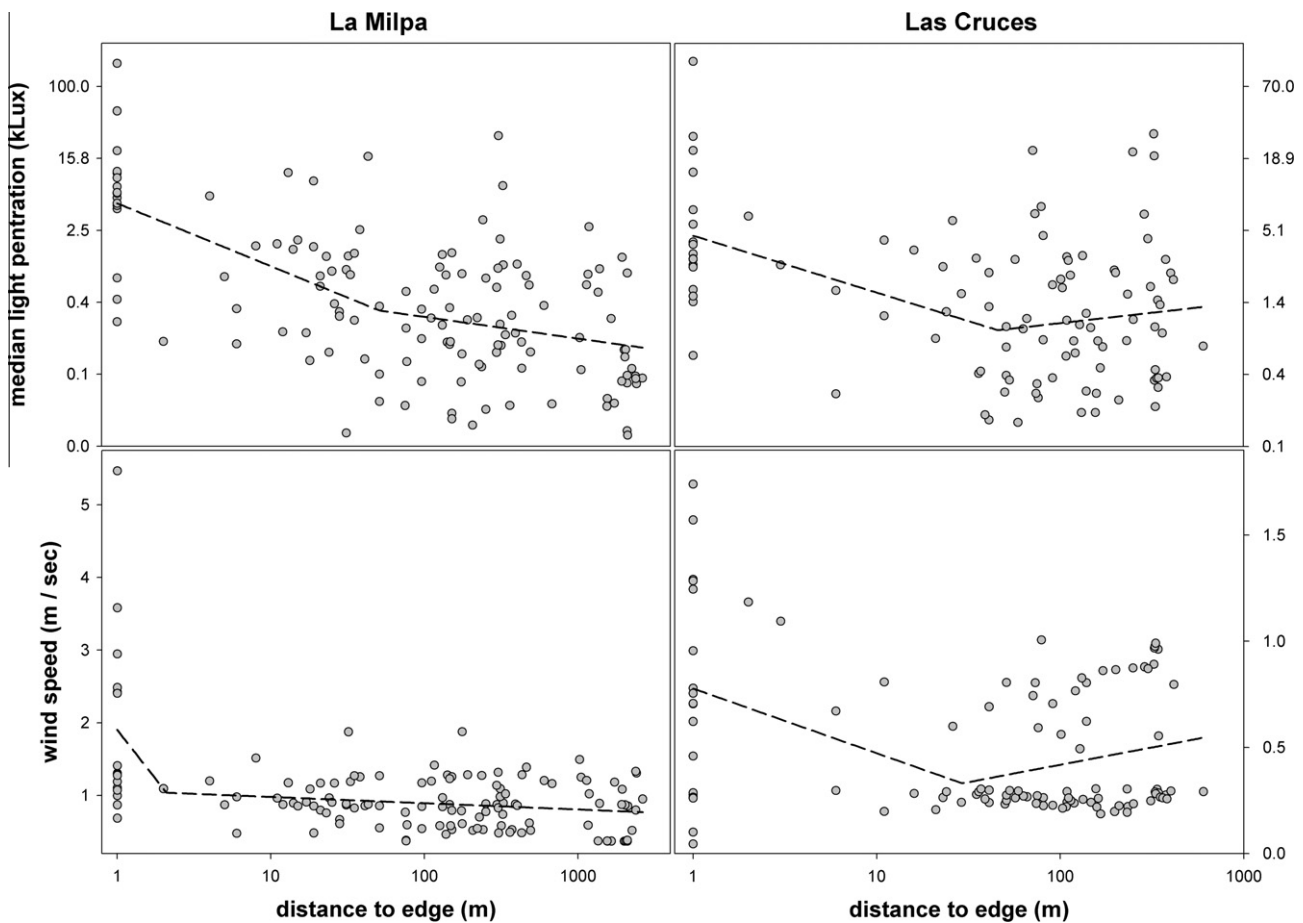
### 3. Results

Avian species composition between adjacent points <100 m apart was not more likely to be similar than species similarity between points >100 m apart (La Milpa:  $t_{122} = 0.69$ ,  $P > 0.45$ ; Las Cruces:  $t_{98} = -1.82$ ,  $P > 0.07$ ), implying that our point count data were sufficiently independent for valid analyses without discarding any points.

Up to a point (see below), light penetration (both median and range) and wind speed decreased with distance from a forested edge (Fig. 1), and canopy cover increased, yet ambient temperature, VPD, and heat index varied little or not at all (Table 1). Heat index exhibited a near identical pattern to ambient temperature, an unsurprising result given the extremely high correlation between the variables (Table 2). In general, other measures were statistically independent, with the possible exception of the light penetration values, as the correlation between median and range values tended to be high (Table 2); moreover, the magnitude and direction of each correlation was similar between sites.

On the basis of the breakpoint of a two-segment piecewise regression, DI varied markedly depending on the microclimate variable and the study site. For example, the DI for wind was anywhere between 2.2 m (La Milpa) and 30.0 m (Las Cruces), and the DI for temperature was between 8.4 m and 239.0 m at the two sites. By contrast, the DI for light penetration was ~50 m at each site (La Milpa, 52.9 m; Las Cruces, 47.0 m). The DI for percent canopy cover, a somewhat correlated measure (La Milpa  $r = -0.61$ ; Las Cruces  $r = -0.52$ ), also varied considerably between sites, being 1.1 m at La Milpa but 40.5 m at Las Cruces.

Because of the high correlation between ambient temperature and heat index (Table 2), it was clear that the latter was not an independent measure of microclimate. To avoid problems of multicollinearity in the multiple regression embedded in CCA, we excluded heat index from our analyses (although its inclusion did not materially alter results along the first ordination axis). Ordinations of species and associated biplots of microclimate were broadly similar for La Milpa and Las Cruces (Fig. 2), and species by microclimate correlations were significant for the first two axes in each case (La Milpa: 0.76,  $P < 0.01$ , and 0.65,  $P < 0.05$ ; Las Cruces: 0.76,  $P = 0.03$ , and 0.72,  $P < 0.04$ ). In particular, at both sites the principal axis was one of light penetration and canopy cover, and the secondary axis captured ambient temperature and VPD. Light penetration was especially “important” (i.e., its loading was high-



**Fig. 1.** Median light penetration and wind speed relative to distance to edge for La Milpa Field Station, Belize (left panels;  $n = 130$  points) and Las Cruces Biological Station, Costa Rica (right panels;  $n = 104$  points). Values on the ordinate have been scaled back to the range of raw values. The dashed line is for a two-segment piecewise regression.

**Table 1**  
Statistical relationship, from ordinary least squares linear regressions, between microclimate variables and distance from a forest edge at La Milpa Field Station, Belize, and Las Cruces Biological Station, Costa Rica.

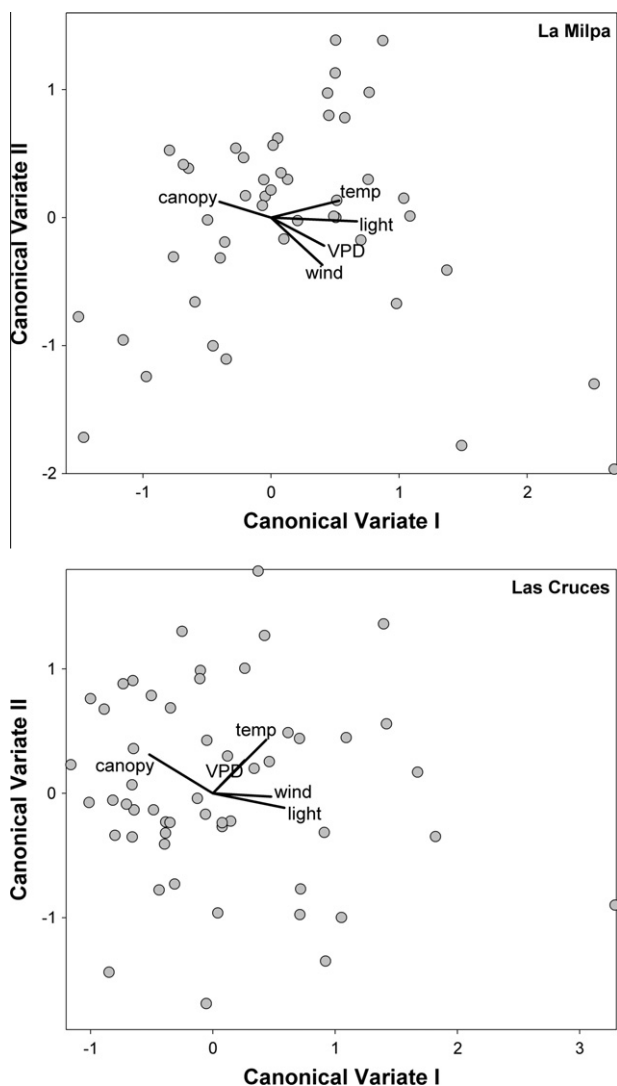
Microclimate variable	La Milpa			Las Cruces		
	<i>m</i>	<i>b</i>	<i>r</i> <sup>2</sup>	<i>m</i>	<i>b</i>	<i>r</i> <sup>2</sup>
Median light penetration	-0.29	0.57	0.33	-0.23	0.37	0.14
Range of light penetration	-0.29	0.56	0.16	-0.30	0.49	0.11
Wind speed	-0.28	0.55	0.21	-0.12	0.19	0.09
Ambient temperature	-1.41	2.73	0.07	0.07	-0.11	0.002
Vapor pressure deficit	-0.10	0.19	0.02	0.02	-0.003	<0.001
Heat index	-2.05	3.99	0.07	0.12	0.20	0.004
Percent canopy cover	0.11	0.74	0.11	0.14	0.78	0.14

est) along the first axis (Table 3). On a species-by-species basis, mean light penetration correlated weakly with mean distance from a forest edge (Fig. 3); in other words, the light environment a given species occupied was not necessarily associated with the distance from the edge at which that species occurred (61.9% of cases at La Milpa, 55.7% at Las Cruces).

The light environment of a species (i.e., its score on the first CCA axis) was a good predictor of that species' regional vulnerability to extirpation (Fig. 4). For La Milpa, species that occupied well-lit habitats exhibited no distinct pattern in population trends (slope = 0.03,  $P > 0.20$ ), but species that occupied poorly-lit habitats—those with little light penetration—tended to have negative population trends (slope = -0.08,  $P < 0.05$ ; Fig. 4). We could not perform a

**Table 2**  
Correlation matrix of microclimate variables at La Milpa Field Station, Belize (top rows;  $n = 130$  points), and Las Cruces Biological Station, Costa Rica (bottom rows;  $n = 104$  points).

	Ambient temperature	Vapor pressure deficit	Heat index	Wind speed	Light penetration	Light range
Vapor pressure deficit (hPA)	0.789					
Heat index (°C)	0.755	0.768				
Wind speed (m/s)	0.989	0.704	0.067			
Light penetration (kLux)	0.043	0.088	0.017			
Light range (kLux)	0.016	0.182	0.436	0.418		
Canopy cover (%)	0.453	0.477	0.441	0.401		
	0.354	0.386	0.359	0.292	0.687	
	0.411	0.499	0.393	0.386	0.856	
	-0.190	-0.251	-0.159	-0.203	-0.608	-0.415
	-0.191	-0.268	-0.193	-0.284	-0.522	-0.439



**Fig. 2.** Canonical correspondence analysis ordination of bird species for La Milpa Field Station, Belize ( $n = 46$  species), and Las Cruces Biological Station, Costa Rica ( $n = 54$  species), with key microclimate variables displayed as a biplot. Note that, at either site, there is a fairly clear light penetration and percent canopy cover axis versus a less clear axis that represents the other microclimate variables.

regression analysis on Las Cruces data because only qualitative scores of population trend were available; nonetheless, the tendency for species in low-light habitats to be more vulnerable is clear from visual inspection of the plot (Fig. 4). Trend data were not available for all species, but, species-for-species, the correlation between regional population trend and light environment tended to support the hypothesis that species that occupy low-light environments are more vulnerable (La Milpa:  $r = -0.23$ ,  $n = 44$ ; Las Cruces:  $r = -0.29$ ,  $n = 34$ ).

#### 4. Discussion

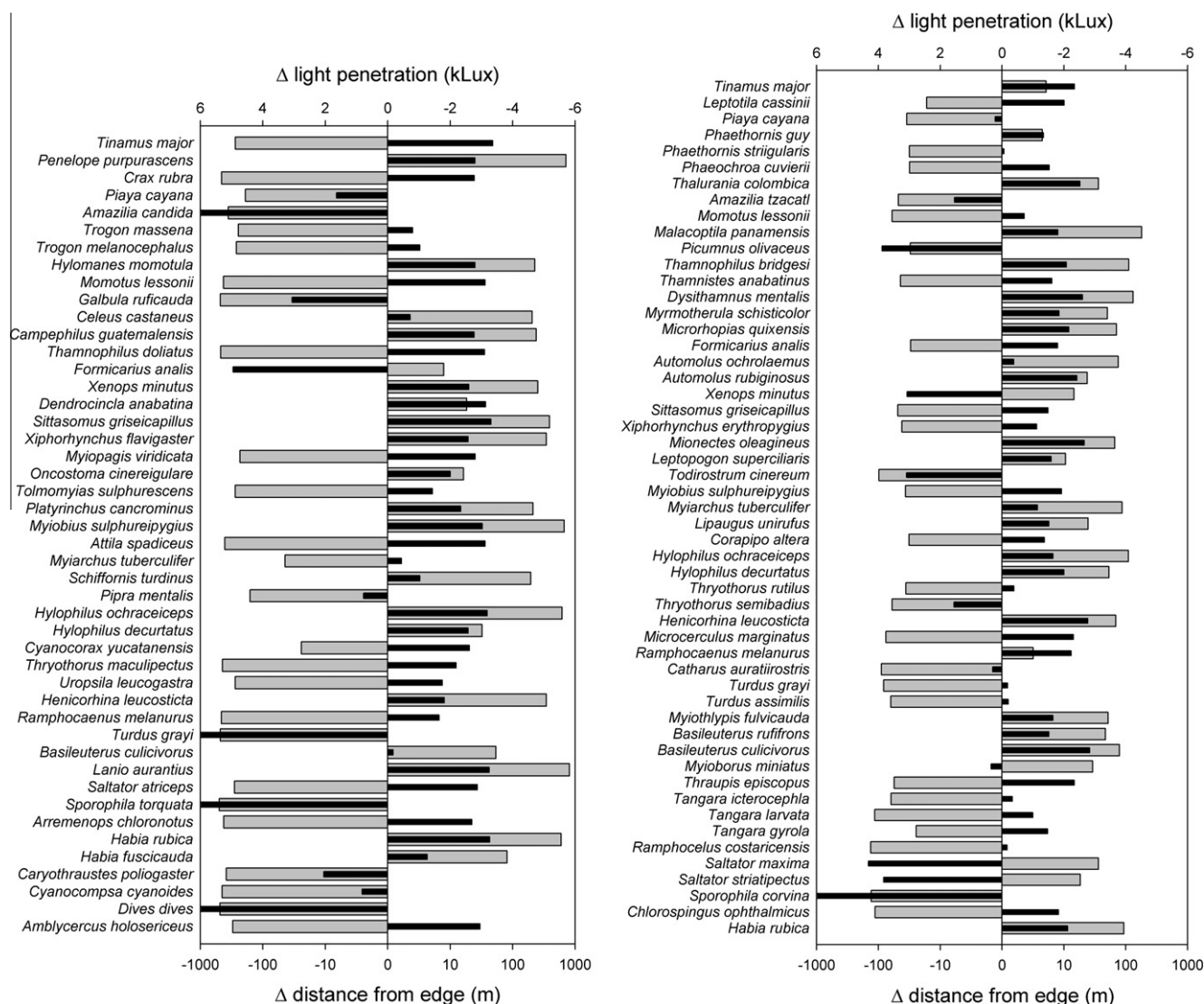
Studies of how microclimate varies with distance into a forest from an edge have had some mixed results, but have generally agreed that interior forests are relatively cool, moist, calm, and dark places. The general concordance of our results to past studies and the similar findings across both of our study sites lends confidence to our ability to detect real differences in microclimate relative to deforested edges in lowland and foothill tropical forests. Turner (1996), Chen et al. (1999), Newmark (2001), and others

indicated that ambient temperature decreased away from edge, although we found that it stabilized quickly from an edge, and Young and Mitchell (1994) found that it fluctuated by season and aspect. Similarly mixed results have come from air moisture measurements (relative humidity, VPD, etc.), which likely are also affected by season and aspect (*sensu* Young and Mitchell, 1994). Additional difficulties have sprung from presentation of results when, for example, a study's statistical presentation indicates stabilization, but those results do not correspond to the paper's graphical presentation (Stevens and Husband, 1998). Our results indicated that like temperature, VPD remained relatively stable as one moved into the forest from an edge, although it is worth mentioning the slight increase seen at Las Cruces, which is explained by its being a rather mesic forest overall.

We found that wind speed and light intensity tended to decrease away from an edge, and that percent canopy cover increased, which is not surprising given canopy cover's well-documented negative correlation with light penetration. Light penetration, in particular, exhibited a strong edge influence, with a DI of  $\sim 50$  m (Fig. 1). Young and Mitchell (1994;  $\sim 50$  m DI) and Davies-Colley et al. (2000;  $\sim 40$  m DI) had similar results when investigating photosynthetically active radiation, a measurement akin to our light intensity metric. In other words, the light environment of a forest is altered up to 50 m from a forest's edge (within the outer [0–10 m] and inner [10–50 m] edge zones, *per* Young and Mitchell, 1994), effectively meaning the footprint of deforestation is larger than the area cleared alone. By Young and Mitchell's (1994) calculations a fragment would need to be  $>9$  ha to be removed from the 50-m DI, and that a patch  $<1$  ha would be completely dominated by the edge zone, i.e., having no interior microclimate zone.

Our light intensity results provide the best support to date for the hypothesis that sensitivity to light is a key factor that limits occurrence of tropical forest species (Théry, 2001), including tropical birds near forest edges (Stratford and Robinson, 2005; Lindell et al., 2007; Patten and Smith-Patten, 2009). Not only is light penetration the key microclimate variable associated with the bird assemblage at our study sites in Belize and Costa Rica (Fig. 2), but it is clear that particular bird species are associated with high- and low-light environments (Fig. 3). Although not experimentally verified yet, our data do point to light environment and sensitivity to that environment, perhaps via physiological or behavioral constraints, as a plausible mechanism for extirpation in a deforested or disturbed tropical forest. Our inference is supported by being able to associate regional declines of these same species to the light environment the species occupies: species whose populations have declined markedly across the forested Petén region (e.g., Patten et al., 2010; Patten and Smith-Patten, 2011) and across the forested portions of Costa Rica and western Panama (e.g., Robinson, 2001; Sigel et al., 2010) tend to be those species that occur in low-light environments (Fig. 4). For example, *Malacoptila panamensis*, *Microrhopias quixensis*, *Myiobius sulphureipygius*, and *Hylophilus ochraceiceps* occur in low-light environments and their populations have declined in both regions. We conclude that in addition to direct loss of habitat in an increasingly deforested region, alteration of the light environment, through increased light penetration, can lead to the decline in regional populations of many forest bird species.

Light environment itself is complex and certainly there are many edge effects that can alter it and perpetuate a feedback loop. For example, our study was limited to microclimate within 2 m of the ground, but many tropical bird species occupy forest strata well above the ground (Parker et al., 1996), and research has shown that microclimate of tropical forest canopies may be desiccated  $>2$  km from an edge (Briant et al., 2010). Desiccation will lead to leaf loss, which will increase light penetration and lead to further desiccation. Accordingly, although we found a DI of  $\sim 50$  m



**Fig. 3.** Difference scores (for points on which species were recorded and not recorded) for mean light environment (black bar) and mean distance from a forest edge (gray bar) at La Milpa Field Station, Belize, and Las Cruces Biological Station, Costa Rica. If the light environment is a simple, linear function of distance from edge, then the difference scores would coincide (i.e., black and gray bars would overlap).

**Table 3**

Loadings, correlations between the raw variables and synthetic variates from a canonical correspondence analysis (CCA), for microclimate variables at La Milpa Field Station, Belize, and Las Cruces Biological Station, Costa Rica. As a rule, a loading > |0.32| can be interpreted as a meaningful correlation—i.e., the variate (axis) captures a substantial amount of variation in the raw variable—with a loading > |0.71| accounting for 50% overlapping variance (Tabachnick and Fidell 2007:649). At both sites, median light penetration is the key raw variable captured on the first CCA axis.

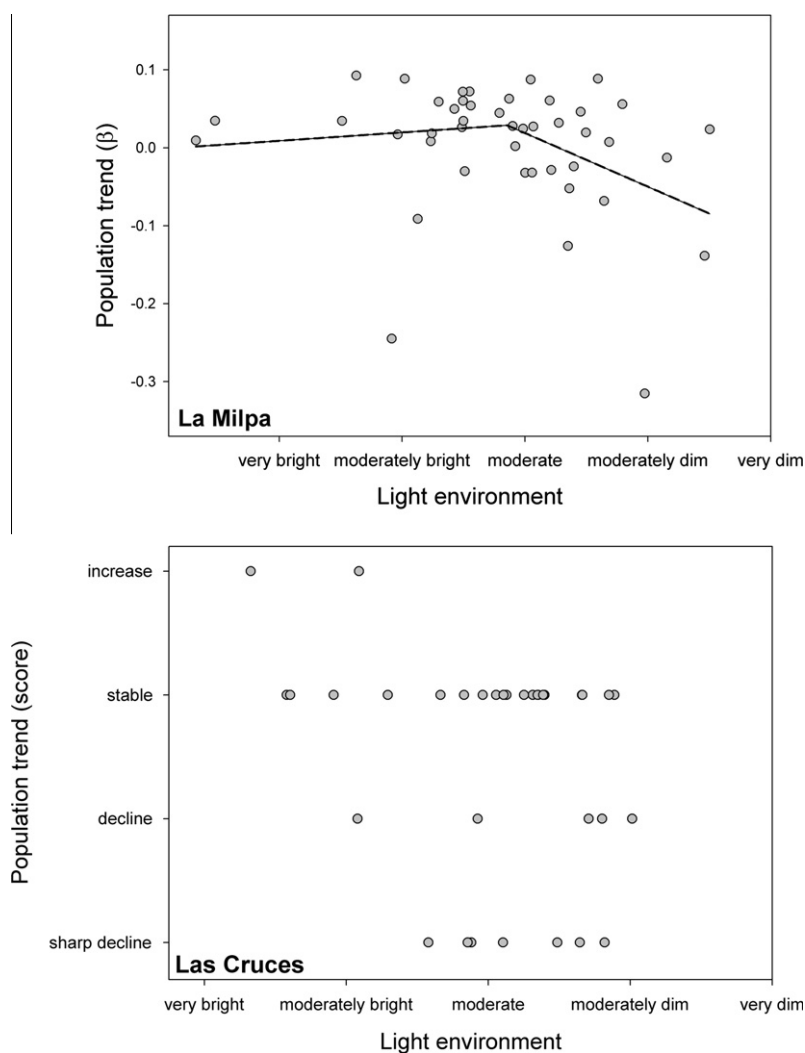
Microclimate variable	La Milpa		Las Cruces	
	Axis 1	Axis 2	Axis 1	Axis 2
Median light penetration (kLux)	0.905	−0.043	0.765	−0.176
Range of light penetration (kLux)	0.603	0.190	0.713	−0.019
Wind speed (m/s)	0.539	−0.568	0.623	−0.041
Ambient temperature (°C)	0.717	0.204	0.570	0.654
Vapor pressure deficit (hPa)	0.559	−0.337	0.341	0.404
Canopy cover (%)	−0.543	0.191	−0.680	0.474

for light penetration, the actual DI may be much greater if we could factor in microclimate changes up to the canopy.

In addition to canopy moisture, various studies have demonstrated that soil moisture increases steeply away from an edge

(Camargo and Kapos, 1995; Gehlhausen et al., 2000). Soil moisture affects which plant species can grow in a particular area, and it may be that a change in soil moisture will lead to a change in dominant tree species. It is already well established that tree species composition changes near a forest edge (Lopes et al., 2009; Tabarelli et al., 2010), with species richness declining away from an edge (Gehlhausen et al., 2000) and higher species turnover near (<60 m) an edge (Laurance et al., 1998). Foliage density changes with tree species and age within species (Lieberman et al., 1989; Kabakoff and Chazdon, 1996), as well as with height of woody vegetation (Montgomery and Chazdon, 2001). These results lead us to suggest that a turnover in tree species near an edge will further alter light penetration, perhaps in a non-additive way given increased desiccation of the canopy nearer to an edge (Briant et al., 2010).

Another interaction that may alter the DI of light penetration, VPD, ambient temperature, and other microclimate parameters is the role of other species in the ecosystem. For example, the presence of a leaf cutter ant (*Atta* sp.) colony alters microclimate ~200 m<sup>2</sup> around the nest (Meyer et al., 2011), and colonies are not distributed randomly through a tropical forest but instead



**Fig. 4.** Vulnerability to extirpation as a function of light environment. Trend estimates are from studies in the same biogeographic regions as La Milpa Field Station, Belize, and Las Cruces Biological Station, Costa Rica (see text). For the La Milpa data, the line represents results of a two-segment piecewise regression.

are more common at or near edges (Wirth et al., 2007). All else being equal, if creation of an edge lures leaf cutter ants to start a colony there and that colony's existence alters microclimate around it, then microclimate near an edge will change above and beyond the abiotic “distance from edge” patterns we found. Additional interactions may arise from increases or decreases in predators and food resources at forest edges. Edges may attract higher numbers of or facilitate increased activity of various nest predators, especially snakes (Chalfoun et al., 2002), and altered light penetration may disrupt male displays (Théry, 2001). As for food, arthropod richness and abundance exhibit a clear edge influence (Magura et al., 2001; Van Wilgenburg et al., 2001; Prinzing, 2005), and fruiting trees tend to be more common near forest edges (Cubiña and Aide, 2001). Lastly, the type of edge affects microclimate variation, as forest edges that border agricultural fields exhibit sharper changes in microclimate than do edges that border at least scattered trees (Gehlhausen et al., 2000), and edge age affects the strength and distance of an edge influence, given that edges up to 50 years old may continue to exhibit an edge influence (Matlack, 1994).

Potential ecological interactions and complications aside, our results indicate an environmental explanation of why some species of tropical birds are more vulnerable to habitat loss and fragmentation than other species. It remains to be determined whether a

given species does not occur in forest with increased light penetration as the result of a physiological constraint—simply from having sensitive eyes (Fig. 3; see also Stratford and Robinson, 2005; Ibarra-Macia et al., 2011) or from extra-retinal light that affects health, including changes in reproduction and molt (e.g., Menaker et al., 1970)—or because that species avoids forests with increased light penetration for reasons associated with habitat selection cues—i.e., increased light creates a perceptual trap for the species (Patten and Kelly, 2010). Regardless, we concur with Théry (2001) that “measurements of light spectra may therefore provide an estimate of the structural impact of forest exploitation,” and we further suggest that such measures will be an index of vulnerability to extirpation of forest-dependent species.

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