Biological Conservation 155 (2012) 85–93

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

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

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ARTICLE INFO

Article history:
Received 29 February 2012
Received in revised form 26 May 2012
Accepted 1 June 2012
Available online 17 July 2012

Keywords:
Belize
Costa Rica
Extinction
Light environment
Microclimate
Neotropics
Population trend
Risk

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 censussed 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.

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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http://dx.doi.org/10.1016/j.biocon.2012.06.004

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 censussed 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 ⩾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.