



Guild-level responses of bats to habitat conversion in a lowland Amazonian rainforest: species composition and biodiversity

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Landscape modification represents one of the most severe threats to biodiversity from local to global scales. Conversion of forest to agricultural production generally results in patches of habitat that subdivide or isolate populations, alter the behavior of species, modify interspecific interactions, reduce biodiversity, and compromise ecosystem processes. Moreover, conversion may increase exposure of humans to zoonoses to which they would otherwise rarely be exposed. We evaluated the effects of forest conversion to agriculture, and its subsequent successional dynamics, on bat communities in a region of the Amazon that was predominantly closed-canopy rainforest. Based on a nonmanipulative experiment, we quantified differences in species composition, community structure, and taxonomic biodiversity among closed-canopy forest (bosque), agricultural lands (chacra), and secondary forest (purma) for two phyllostomid guilds (frugivores and gleaning animalivores) during the wet and dry seasons. Responses were complex and guild-specific. For frugivores, species composition (species abundance distributions) differed between all possible pairs of habitats in both wet and dry seasons. For gleaning animalivores, species composition differed between all possible pairs of habitats in the dry season, but no differences characterized the wet season. Ecological structure (rank abundance distributions) differed among habitats in guild-specific and season-specific manners. For frugivores, mean diversity, evenness, and dominance were greater in bosque than in purma; mean dominance was greater in bosque than in chacra, but local rarity was greater in chacra than in bosque, and no differences were manifest between purma and chacra. For gleaning animalivores, mean diversity and evenness were greater in bosque than in purma, but no differences were manifest between chacra and bosque, or between purma and chacra. Such results have important implications for management, conservation, and the epidemiology of zoonotic diseases.

La actual modificación del paisaje, a escalas que van de lo local a lo global, es una de las amenazas más severas a la biodiversidad. De manera general, la conversión de bosques a áreas agrícolas produce parches de hábitat que subdividen o aíslan poblaciones, alteran la conducta de las especies, modifican las interacciones interespecíficas, reducen la biodiversidad y comprometen las funciones de los ecosistemas. Más aún, la transformación de estos ambientes puede incrementar la probabilidad de que las poblaciones humanas interactúen con zoonosis con las que de otra manera raramente entrarían en contacto. Evaluamos los efectos de la conversión de hábitat en comunidades de murciélagos en una región de Amazonia en la que la vegetación dominante es un bosque lluvioso de copas cerradas, y en la cual los efectos de la conversión a usos agrícolas sobre la biodiversidad, y la subsecuente dinámica sucesional, son aún poco comprendidos. Por medio de un experimento no-manipulativo, cuantificamos las diferencias en composición de especies, estructura de la comunidad y diversidad taxonómica entre bosque cerrado (bosque), áreas agrícolas (chacra) y bosque secundario (purma) para dos gremios tróficos de murciélagos

filostómidos (frugívoros y forrajeadores de sustrato) durante dos temporadas (secas y lluvias). Las respuestas fueron complejas y diferentes para cada gremio. Para los frugívoros, la composición de especies (distribución de las abundancias) fue diferente para todos los posibles pares de hábitats tanto para secas como para lluvias. Para los forrajeadores de sustrato, la composición de especies difirió entre todos los posibles pares de hábitats en la temporada seca, pero no en la de lluvias. La estructura ecológica (distribuciones rango-abundancia) fue también específica para gremios y temporadas. Para los frugívoros, la diversidad promedio, equidad y dominancia fueron mayores en bosque que en purma; la dominancia promedio fue mayor en bosque que en chacra, pero la rareza local fue mayor en chacra que en bosque, y no se encontraron diferencias entre purma y chacra. Para los forrajeadores de sustrato, la diversidad promedio y la dominancia fueron mayores en bosque que en purma, pero no se detectaron diferencias entre chacra y bosque, o entre purma y chacra. Estos resultados tienen importantes implicaciones para el manejo, conservación y epidemiología de zoonosis.

Key words: agriculture, biodiversity, Chiroptera, frugivore, gleaning animalivore, habitat conversion, Neotropics, species composition, successional forest

Habitat fragmentation and conversion to agriculture, along with climate change, are among the human activities that represent the greatest threats to the conservation of biodiversity at local, regional, and global scales (Sala et al. 2000; Newbold et al. 2015; Betts et al. 2017). Fragmentation creates patches of habitat and subdivides or isolates populations (Hanski et al. 1995), thereby altering the behavior of species (Hargis et al. 1999), modifying interspecific interactions (Aizen and Feinsinger 1994), reducing biodiversity (Vie et al. 2009; Newbold et al. 2014), and compromising ecosystem processes (Cardinale et al. 2006; Jones et al. 2009). Moreover, habitat conversion typically occurs in proximity to human settlements. Such modified landscapes may affect ecological interactions associated with pathogen transmission by differentially altering the abundance of species and composition of ecological communities that represent vectors or reservoirs of disease (Ostfeld and LoGiudice 2003).

Unfortunately, the rate of habitat conversion and fragmentation associated with anthropogenic activities is increasing (e.g., Vitousek et al. 1997; Monastersky 2015), especially in the Neotropics, which harbors a considerable proportion of the world's species (Heywood and Watson 1995). Indeed, the Anthropocene will become increasingly characterized by a mosaic of human-modified habitats, with a concomitant need for decision makers to explicitly consider the conservation value of such habitats in designing effective conservation networks to preserve species and promote biodiversity (Chazdon et al. 2009; Van de Perre et al. 2018). To do otherwise enhances the likelihood that the earth will experience its sixth mass extinction (Ceballos et al. 2015).

In the New World, biodiversity of bats increases rapidly toward the equator, including increases in taxonomic (Stevens and Willig 2002), functional (Stevens et al. 2003), and phylogenetic (Stevens 2006) aspects of biodiversity. The increase in functional diversity arises from an increase in the number of foraging guilds, as Neotropical bats include aerial insectivores, high-flying insectivores, nectarivores, frugivores, gleaning animalivores, piscivores, and sanguinivores (Stevens et al. 2003; Stevens 2004). This increase in functional diversity also represents an increase in the importance and number of ecosystem services that are provided by bats (Lacher et al., *In press*).

For example, Neotropical bats are important agents of pollination and seed dispersal for many species of plants (Fleming and Heithaus 1981; Galindo-González et al. 2000), and their activity promotes secondary succession of disturbed areas (Guariguata and Ostertag 2001; Muscarella and Fleming 2007).

Bats exhibit complex responses to habitat conversion, loss, and fragmentation that are often species-specific (Cosson et al. 1999; Schulze et al. 2000; Clarke et al. 2005; Castro-Arellano et al. 2007; Harvey and González Villalobos 2007; Willig et al. 2007; Klingbeil and Willig 2010), and depend on the focal scale of analysis (Gorresen et al. 2005; Pinto and Keitt 2008; Klingbeil and Willig 2009; Avila-Cabadilla et al. 2012), as well as on the extent and intensity of habitat conversion in the region (Presley et al., *In press*). Intensive and extensive habitat conversion may produce homogeneous landscapes with a low diversity of abundant resources, resulting in communities with relatively low biodiversity (Menge et al. 1985; Fuhlendorf and Engle 2001). In contrast, a moderate level of habitat conversion may increase landscape heterogeneity, facilitating habitat and resource diversity, and supporting communities with high biodiversity (e.g., Meyer et al. 2008; Cisneros et al. 2015; Farneda et al. 2015). Consequently, the ways in which species composition and biodiversity change in response to habitat conversion (e.g., forest to agriculture) and subsequent secondary succession after abandonment are challenging to predict.

Responses of bats to habitat conversion may be guild- (Harvey and González Villalobos 2007; Meyer and Kalko 2008; Klingbeil and Willig 2009; Avila-Cabadilla et al. 2012; García-Morales et al. 2013; Arroyo-Rodríguez et al. 2016) or season-specific (Klingbeil and Willig 2010; Cisneros et al. 2015), and are driven by effects of landscape characteristics (i.e., the composition and configuration of native and converted land uses). These responses also depend on the diversity and abundance of resources that are available for each guild. Frugivorous bats generally increase in abundance and in taxonomic biodiversity in response to low-to-moderate levels of deforestation because the plant species on which they forage thrive in forest openings and along forest edges (e.g., Lobova et al. 2003; Thies and Kalko 2004; Castro-Luna and Galindo-González 2011). In contrast, gleaning animalivores typically decrease in abundance and biodiversity in response to the loss of closed-canopy

forest (Klingbeil and Willig 2009; Farneda et al. 2015). These bats forage primarily in habitats between the canopy and the understory (Fenton et al. 1992; Meyer et al. 2008), which are uncommon habitats in agricultural and early successional forests. In addition, seasonal changes in resource availability affect the compositions of local communities and how bats use the landscape, and may do so in species- (Cosson et al. 1999; Schulze et al. 2000; Clarke et al. 2005; Harvey and González Villalobos 2007) or guild-specific fashions (e.g., Harvey and González Villalobos 2007; Meyer and Kalko 2008; Klingbeil and Willig 2009; Avila-Cabadilla et al. 2012; García-Morales et al. 2013; Cisneros et al. 2015; Arroyo-Rodríguez et al. 2016). Flight allows bats to track spatial fluctuations in resources over time, both within and among landscapes, via short- to moderate-distance movement or by increasing their home range size to meet dietary needs (Fleming and Eby 2003).

We used a nonmanipulative experiment to evaluate the effects of habitat conversion (i.e., closed-canopy tropical forest converted to agriculture and subsequent abandonment to early successional forest) on frugivorous and gleaning animalivorous bats in the Peruvian Amazon. More specifically, we determined 1) if the composition of each guild changed in response to habitat conversion and succession, 2) if habitat conversion and succession affected biodiversity within each guild, and 3) if these effects were consistent throughout the year or were season-specific.

Based on differences among habitat types in plant species composition and physiognomy as well as seasonal variation in productivity, we predicted that: 1) species richness, evenness, and diversity would differ among habitats, with values being greatest in closed-canopy forest, least in agricultural lands, and intermediate in early successional forest; 2) dominance would be greatest in agricultural habitats, least in closed-canopy forest, and intermediate in early successional forests; 3) the structure of taxonomic biodiversity (i.e., rank abundance distributions [RADs]) and species composition (i.e., species abundance distributions [SADs]) would differ between all pairs of habitats; 4) differences would be more pronounced for gleaning animalivores than for frugivores because agricultural lands and early successional forests lack the subcanopy habitat that is typically used by gleaning animalivores; and 5) differences would be more distinct during the wet season than during the dry season because greater abundances of resources would allow species to focus activities in preferred habitats.

MATERIALS AND METHODS

Study area.—This study on guild-level responses of Neotropical bats to habitat conversion complements an evaluation of species-level responses based on the same experimental design and study system (Willig et al. 2007). Research was conducted in lowland Amazonian forest south of Iquitos (3.74°S, 73.24°W) in northeastern Peru (Fig. 1). The climate is warm and humid. Rainfall is substantial (~2,800 mm/year), with a modest dry season (185 mm/month) from June to October and a wet season (292 mm/month) from January to May (Madigovsky and Vatnick 2000).

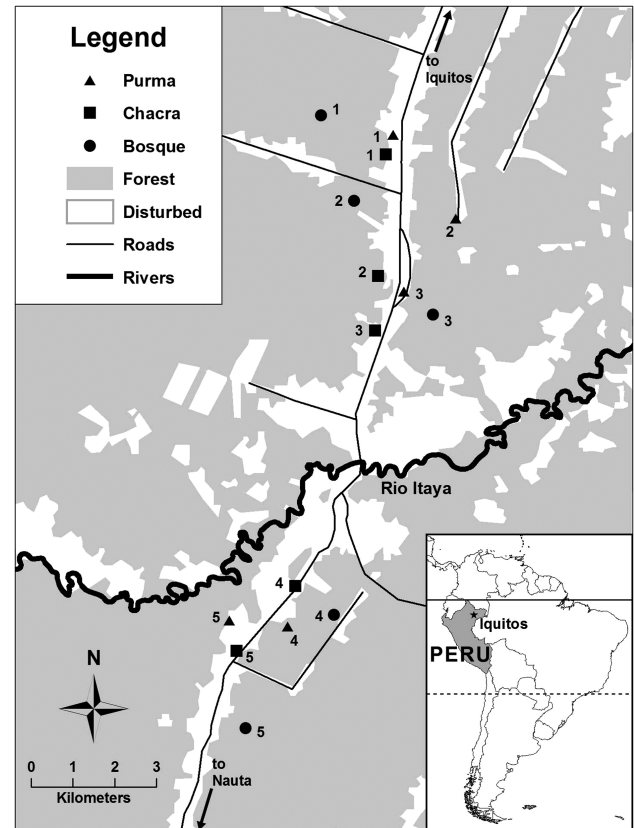


Fig. 1.—Map of environs to the south of Iquitos, Perú, illustrating the extent of deforestation and fragmentation along the Río Itaya and the Iquitos–Nauta Highway. Superimposed on this heterogeneous landscape are five replicate blocks (1–5) that each comprises three plots (bosque, purma, and chacra). The location of Iquitos in Perú, and Perú’s location in South America (Equator, solid horizontal line; Tropic of Capricorn, dashed horizontal line), appear in the insert. Modified from Willig et al. (2007).

Iquitos is in the Inambari area of endemism, which is a conservation priority because it harbors many restricted-range and endemic species (da Silva et al. 2005). Work was conducted along the recently paved highway that connects the cities of Iquitos and Nauta (Mäki et al. 2001). Data were collected during two 5-month periods: July to November 2002 and January to May 2003, corresponding to drier and wetter seasons of the year, respectively (Madigovsky and Vatnick 2000).

Deforestation in the Iquitos region was generally associated with small-scale slash-and-burn subsistence agricultural practices (Supplementary Data SD1). Burning was followed by cultivation, resulting in a plantation, locally called chacra, that covers a few hectares (Mäki et al. 2001; Supplementary Data SD1B). After the soil is no longer fertile, the influx of pioneer species into abandoned chacra during the subsequent 5 to 10 years results in early successional forest that locally is called purma (Mäki et al. 2001; Supplementary Data SD1C). Purma differs dramatically from closed-canopy forest in terms of plant species composition and physical structure (canopy < 10 m tall, dense understory). Closed-canopy lowland forest (hereafter bosque) is characterized by high tree diversity (Vásquez 1997) with a 30-m canopy punctuated by 50-m emergent trees

(Supplementary Data SD1D). Chacra and purma typically have clearly defined boundaries and almost always occur adjacent to bosque (Supplementary Data SD1A). New chacras are typically created next to recently abandoned land that will grow into purma, and in proximity to the dwellings of the people that farm the land.

Field methods.—Five replicate blocks were located along the Iquitos–Nauta Highway between 40 and 70 km SSW of Iquitos, and within 3 km east or west of the road (Fig. 1). Each block contained three plots: one in closed-canopy forest (i.e., bosque), one in agriculture (i.e., chacra), and one in secondary forest (i.e., purma). Because of the heterogeneous landscape and idiosyncratic availability of sites for use, the distances among plots within blocks were variable, as were the distances between plots in adjacent blocks (i.e., average distance between plots within blocks was 1.5 km, whereas the average inter-block distance between plots of the same habitat type was 3.6 km). Each plot was 250 m × 250 m (Supplementary Data SD2) and was sampled for two three-night sessions, one during the dry season and one during the wet season. Sampling effort was constant for all combinations of block, season, and habitat. During the dry season, a different block was selected randomly for sampling each month; the order of sampling remained the same during the wet season to ensure that populations at each plot had the same number of months to recover from removal of individuals during the preceding dry season. On the first night, two interior subplots and two edge subplots were chosen randomly for sampling; on the second night, the remaining four subplots were sampled; and on the third night, two interior and two edge subplots were chosen at random without regard to previous sampling. Each night, three 12 m × 3 m mist nets were erected in each selected subplot, two at ground level and one in the upper understory, directly above one of the ground nets. This design sampled bats flying up to 6 m above the ground.

This work was conducted as part of an NIH grant to evaluate bats as reservoirs for arboviruses; this required the collection of blood and tissues. Consequently, up to 20 individuals of each species at each plot in each season were sacrificed and prepared as standard museum specimens. The resultant specimens were used as a reference collection to verify species identifications. Specimens were deposited in the Museo de Historia Natural of the Universidad Nacional Mayor de San Marcos and in the Natural Science Research Laboratory of Texas Tech University. Individuals of abundant species (primarily *Carollia* spp.) beyond the first 20 captures were released after identification to species. Before release, each individual was marked by fur trimming to prevent it from being counted more than once in estimates of abundance during a particular season. We followed the systematic recommendations of Simmons (2005) for bat taxa in lowland Amazonia, except for recognizing *Carollia benkeithi* (Solari and Baker 2006) as distinct from *Car. Castanea*, *Platyrrhinus incarum* as distinct from *P. helleri* (Velazco et al. 2010), *Gardnerycteris* as a distinct genus from *Mimon* (Hurtado and Pacheco 2014), and in recognizing Micronycterinae, Glyphonycterinae, and Rhinophyllinae as subfamilies of phyllostomid bats (Baker

et al. 2016). Research involving live animals followed the guidelines for the capture, handling, and care of mammals approved by the American Society of Mammalogists (Sikes et al. 2016) and was approved by the Animal Care and Use Committee of Texas Tech University (ACUC# 01084-03). Additional details about the study area and field methods are available in Willig et al. (2007).

Guild classifications and scale.—We classified bats into broad foraging guilds (i.e., aerial insectivores, frugivores, gleaning animalivores, high-flying insectivores, nectarivores, sanguinivores) based on published recommendations (Wilson 1973; Gardner 1977; Stevens et al. 2006). We further characterized species as dominant, common, or rare based on relative abundances. A dominant species was one whose relative abundance was greater than that of all other species (in cases where two or more species were equally dominant, those taxa were considered to be co-dominants). A rare species was one whose relative abundance was $< 1/S$, where S is species richness. All other species (i.e., those not rare or dominant) were considered to be common. These categorizations were applied at two focal scales: plots and treatment categories (defined as the six unique combinations of habitat and season). Because this approach is hierarchical, plot-level descriptions represent characterizations at the α -scale and descriptions at the level of treatment combinations represent characterizations at the γ -scale. Finally, because bosque represents the native vegetation of lowland Amazonia, we identified rare species from bosque (combining data from wet and dry seasons) and quantified the number of such species (R_B) at the α - or γ -scale in other habitats. In doing so, we considered a species that was only captured in chacra or purma to be rare in bosque.

Data analysis.—For each guild, we used a generalized linear mixed-effects model (GLMM—Venables and Ripley 2002) to quantify the effects of habitat type (bosque versus chacra versus purma), season (wet versus dry), and their interaction on each of seven metrics of biodiversity: species richness (i.e., cumulative number of species), Shannon diversity, Camargo evenness, Berger–Parker dominance, local rarity (i.e., number of species with a relative abundance $< 1/S$ within a plot), bosque rarity (i.e., number of species within a plot that were rare in bosque [based on combined seasons]), and total abundance (i.e., cumulative number of individuals regardless of species). For metrics that differed among habitats based on a GLMM, we conducted a posteriori tests (Tukey test with a Holm–Šidák adjustment) to identify consistent differences between all possible pairs of habitat (i.e., in the absence of significant habitat × season interaction) or pairwise differences between all possible pairs of habitat within each season (i.e., in the presence of a significant $H \times S$ interaction). Because such a posteriori tests are less powerful than their associated GLMM and are protected in the sense that a posteriori tests were only executed when GLMMs were significant ($\alpha \leq 0.05$), we considered $P \leq 0.10$ as evidence for significant pairwise differences. Each metric, except for total abundance, was expressed as its numbers equivalent to estimate “true” biodiversity (Jost 2006). Metrics that are species counts (i.e., richness, rarity) are their own

numbers equivalents. This transformation scales dominance so that larger magnitudes of the metric represent lower dominance but higher biodiversity. All GLMMs and associated a posteriori tests were conducted using the R programming environment (R Core Team 2015) and the MASS (Venables and Ripley 2002), nlme (Pinheiro and Bates 2000), or multcomp (Hothorn et al. 2008) libraries. Season was modeled as a repeated measure, habitat was modeled as a between-subject factor, and block was modeled as a random factor to account for natural spatial variation in environmental characteristics. The inclusion of block as a random factor removes spatial variation associated with the distribution of sites through space, effectively accounting for any form (e.g., linear, bimodal) of spatial autocorrelation prior to evaluations of effects of habitat and season on bat biodiversity. Nonetheless, we evaluated spatial autocorrelation for each of our seven metrics of biodiversity separately for each guild and each season using Moran's I in the ape library in R (Paradis and Schliep 2018). We detected no evidence of spatial autocorrelation in 28 analyses of our response variables (P -values 0.155–0.899, mean = 0.601).

For each of the six treatment combinations, we weighted the presence of species by its relative abundance to characterize SADs. We then ordered those values to characterize RADs. Both kinds of distributions reflect γ -scale characteristics, as the data were combined from all constituent plots within a treatment category to estimate relative abundance of species. We consider SADs to represent species composition and RADs to represent the structure of taxonomic biodiversity, in that the various metrics of biodiversity describe the shape of the RADs on which they are based (Supplementary Data SD3). Effects of habitat and season on guild composition (i.e., SAD) and structure (i.e., RAD) were evaluated with separate chi-square randomization tests in Ecosim version 7 (Gotelli and Entsminger 2005). This randomization test provides two advantages over conventional contingency chi-square analysis: results are not sensitive to small expected values, and it is not necessary to specify degrees of freedom (Gotelli and Entsminger 2005). For all analyses, results were considered significant if $P \leq 0.05$.

RESULTS

The chiropteran fauna of Iquitos was taxonomically and ecologically diverse (Table 1). During 90,720 net-meter-hours of sampling, we captured 3,789 bats representing 52 species, 31 genera, five families, and six feeding guilds. Of those, 3,764 individuals, 44 species, 24 genera, and four guilds were phyllostomids, but only 3,620 of them were either frugivores or gleaning animalivores. Two (*Rhinophylla fischeriae* and *Vampyriscus brocki*) of the 12 bat species that are endemic to the Amazon (Marinho-Filho and Sazima 1998; Solari and Baker 2006) were captured in Iquitos (both frugivores), but each was rare in all habitats.

Frugivores.—The 3,308 captured frugivores represented 24 species, 10 genera, and three subfamilies (Table 1). All species were captured in both seasons, and all but two species were captured in all habitats. The exceptions, *Artibeus concolor* and *Chiroderma trinitatum*, were not captured in bosque.

Mean diversity, evenness, dominance, local rarity, and abundance of frugivores differed among habitats in a consistent manner (i.e., significant habitat effect in the absence of a habitat by season interaction), without any evidence of seasonal effects (Fig. 2). Bosque had greater mean diversity, evenness, and dominance than did purma; purma had greater mean abundance than did bosque; and these two habitats did not differ in terms of mean richness, local rarity, or bosque rarity (Supplementary Data SD4). Chacra had greater mean abundance and local rarity than did bosque; bosque had greater mean dominance than did chacra; and mean richness, diversity, evenness, and bosque rarity did not differ between bosque and chacra (Supplementary Data SD4). Purma did not differ from chacra for any metrics of mean biodiversity (Supplementary Data SD4).

Species abundance distributions of the frugivores differed significantly between every combination of season and habitat (Table 2; Supplementary Data SD5). In contrast, differences in RADs (Table 2; Fig. 3), which are not sensitive to the identity of species, were season-specific. During the dry season, the RAD of chacra was indistinguishable from that of purma, but the RAD of each of the disturbed habitat types differed from that of bosque. During the wet season, the only difference in RADs occurred between bosque and chacra. Finally, RADs did not differ between seasons within any habitat type.

Gleaning animalivores.—The 312 captured gleaning animalivores represented 15 species, 10 genera, and three subfamilies (Table 1). All but three species were captured in both seasons. *Lophostoma carrikeri* and *L. silvicolum* were captured only in the wet season, whereas *Chrotopterus auritus* was captured only in the dry season. Eight species were captured in all habitats; four species were captured in two habitats (bosque and chacra or bosque and purma); and three species (i.e., *L. carrikeri*, *Micronycteris minuta*, and *Phyllostomus discolor*) were captured in only one habitat (chacra).

Mean richness, diversity, evenness, and bosque rarity of gleaning animalivores differed among habitats in a consistent manner (i.e., significant habitat effect in the absence of a habitat by season interaction), without any evidence of seasonal differences (Fig. 4). Bosque had greater mean diversity and evenness than did purma, but mean richness, dominance, local rarity, and bosque rarity did not differ between the two habitats (Supplementary Data SD4). Bosque and chacra did not differ in terms of mean richness, diversity, evenness, dominance, local rarity, or bosque rarity (Supplementary Data SD4). Similarly, purma and chacra did not differ in terms of mean richness, diversity, evenness, dominance, local rarity, or bosque rarity (Supplementary Data SD4). In contrast, mean differences in abundance among habitats were season-specific (Fig. 4). In the wet season, all pairwise differences in mean abundance between habitats were significant. In the dry season, pairwise differences in mean abundance characterized chacra and bosque, and chacra and purma, but not bosque and purma (Supplementary Data SD4).

Species abundance distributions of gleaning animalivores differed between habitats in a season-specific manner: all pairwise comparisons between habitats were significant in the dry season, whereas no pairwise comparison between habitats was

Table 1.—List of bat species in the gleaning animalivore or frugivore guilds, their associations with treatment categories defined by combinations of season (wet or dry) and habitat (bosque, purma, or chacra), and their classification as rare species based on their relative abundance (< 1/S) in bosque (seasons combined).

Subfamily (guild) Species	Species code	Rare in bosque	Wet season			Dry season		
			Bosque	Purma	Chacra	Bosque	Purma	Chacra
Micronycterinae (gleaning animalivores)								
<i>Micronycteris minuta</i>	Mimi	X			X			
Phyllostominae (gleaning animalivores)								
<i>Chrotopterus auritus</i>	Chau	X				X		X
<i>Gardnerycteris crenulatum</i>	Gacr		X	X	X	X	X	X
<i>Lophostoma brasiliense</i>	Lobr	X	X					X
<i>Lophostoma carrikeri</i>	Loca	X			X			
<i>Lophostoma silvicolum</i>	Losi		X	X	X	X	X	X
<i>Phylloderma stenops</i>	Phst	X	X			X		X
<i>Phyllostomus discolor</i>	Phdi	X			X			X
<i>Phyllostomus elongatus</i>	Phel	X	X	X	X	X		X
<i>Phyllostomus hastatus</i>	Phha		X	X	X	X	X	X
<i>Tonatia saurophila</i>	Tosa		X	X	X	X		X
<i>Trachops cirrhosus</i>	Trci	X	X	X	X	X	X	X
Caroliinae (frugivores)								
<i>Carollia benkeithi</i>	Cabe	X	X	X	X	X	X	X
<i>Carollia brevicauda</i>	Cabr		X	X	X	X	X	X
<i>Carollia perspicillata</i>	Cape		X	X	X	X	X	X
Glyphonycterinae (gleaning animalivores)								
<i>Glyphonycteris daviesi</i>	Glda	X	X	X			X	
<i>Glyphonycteris sylvestris</i>	Glsy	X	X		X		X	
<i>Trinycteris nicefori</i>	Trni	X	X	X	X	X		
Rhinophyllinae (frugivores)								
<i>Rhinophylla fischeriae</i>	Rhfi	X	X	X	X	X	X	X
<i>Rhinophylla pumilio</i>	Rhpu		X	X	X	X	X	X
Stenodermatinae (frugivores)								
<i>Artibeus anderseni</i>	Aran	X	X	X	X	X	X	X
<i>Artibeus concolor</i>	Arco	X			X		X	
<i>Artibeus gnomus</i>	Argn	X	X	X	X	X	X	X
<i>Artibeus lituratus</i>	Arli	X	X	X	X	X	X	X
<i>Artibeus obscurus</i>	Arob		X	X	X	X	X	X
<i>Artibeus planirostris</i>	Arpl		X	X	X	X	X	X
<i>Chiroderma trinitatum</i>	Chtr	X		X	X		X	
<i>Chiroderma villosum</i>	Chvi	X	X	X	X			X
<i>Mesophylla macconnelli</i>	Mema	X	X	X	X	X	X	X
<i>Platyrrhinus brachycephalus</i>	Plbr	X		X	X	X	X	
<i>Platyrrhinus incarum</i>	Plin	X	X	X	X	X	X	X
<i>Sturnira lilium</i>	Stli	X	X	X	X	X	X	X
<i>Sturnira magna</i>	Stma	X	X	X	X	X	X	X
<i>Sturnira tildae</i>	Stti	X	X	X	X	X	X	X
<i>Uroderma bilobatum</i>	Urbi	X	X	X	X	X	X	X
<i>Uroderma magnirostrum</i>	Urma	X		X	X	X		X
<i>Vampyressa thuyone</i>	Vath	X	X	X	X	X		X
<i>Vampyriscus bidens</i>	Vabi	X	X	X	X	X	X	X
<i>Vampyriscus brocki</i>	Vabr	X		X	X		X	X

significant in the wet season (Table 3; Supplementary Data SD6). SADs differed between seasons within bosque and within chacra, but did not do so within purma. In contrast, RADs did not generally differ between habitats within seasons or between seasons within habitats (Table 3; Fig. 5) with a single exception (i.e., RAD of bosque differed from that of purma in the dry season).

DISCUSSION

Early research on conservation of tropical forests focused on the need to preserve pristine or closed-canopy forest to protect biodiversity (e.g., Terborgh 1992). More recent perspectives suggest that the luxury of ensuring species preservation by conserving only pristine habitat is no longer feasible (Chazdon

et al. 2009; Reed et al. 2016), in part because of the critical need to convert such land to agricultural production or to allow some anthropogenic use to support growing local human populations (Sunderland et al. 2007; Rao et al. 2016). Moreover, successional forests as well as structured production landscapes that contain a mix of agriculture, successional forest, and closed-canopy forest can contribute to conservation goals by increasing regional populations, buffering species from stochastic events, and providing corridors between islands of closed-canopy forest (Chazdon 2014; Chazdon et al. 2016; Van de Perre et al. 2018). Indeed, agricultural lands and successional forests in lowland Amazonia can contribute resources that support local populations or contribute to landscape-wide persistence of bat species (Willig et al. 2007). For example, no frugivorous or gleaning animalivorous bat species from this study was found

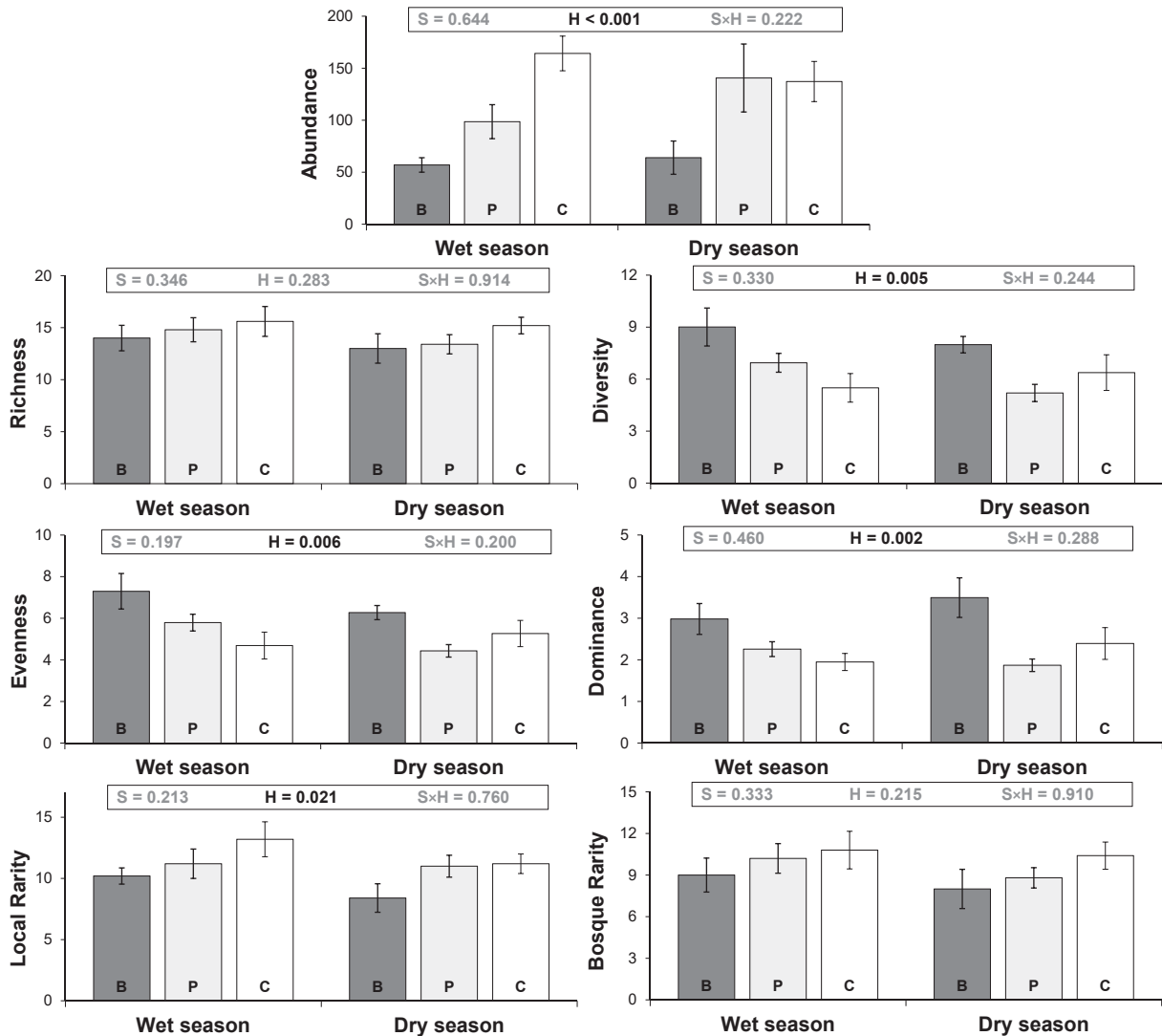


Fig. 2.—Bar diagrams representing mean aspects of frugivore biodiversity (α -level analyses) for combinations of habitat (B, dark shading, bosque; P, light shading, purma; C, no shading, chacra) and season. *P*-values for treatment effects (S, season; H, habitat; S \times H, season by habitat interaction) appear in horizontal frames above bar diagrams, with significance ($P \leq 0.05$) indicated by black letters and nonsignificance ($P > 0.05$) by gray letters. Although error bars ($\pm 1 SE$) represent measures of dispersion for means within each treatment combination, statistical analyses (GLMMs) were based on repeated measures and do not necessarily reflect the nonoverlap of these error bars. Metrics of biodiversity are reported as numbers equivalents.

Table 2.—Results of chi-square tests comparing species abundance distributions or rank abundance distributions of frugivores for each combination of season and habitat (γ -level of analysis). Chi-square values are in the lower triangle; *P*-values are in the upper triangle. *P*-values are based on a Monte Carlo simulation using 10,000 iterations. Significant ($P \leq 0.05$) results are in bold.

Season	Habitat	Dry season			Wet season		
		Bosque	Chacra	Purma	Bosque	Chacra	Purma
Species abundance distribution							
Dry	Bosque	—	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	Chacra	153.5	—	< 0.001	< 0.001	< 0.001	< 0.001
	Purma	184.2	89.6	—	< 0.001	< 0.001	< 0.001
Wet	Bosque	53.3	94.7	142.5	—	< 0.001	< 0.001
	Chacra	165.0	81.7	93.1	136.9	—	< 0.001
	Purma	119.7	110.8	83.7	97.6	96.7	—
Rank abundance distribution							
Dry	Bosque	—	< 0.001	< 0.001	0.543	< 0.001	< 0.001
	Chacra	53.9	—	0.407	0.002	0.377	0.381
	Purma	81.6	20.9	—	< 0.001	0.973	0.429
Wet	Bosque	17.9	41.0	54.0	—	< 0.001	0.196
	Chacra	81.8	23.4	13.1	62.7	—	0.646
	Purma	49.6	23.4	22.5	27.0	20.3	—

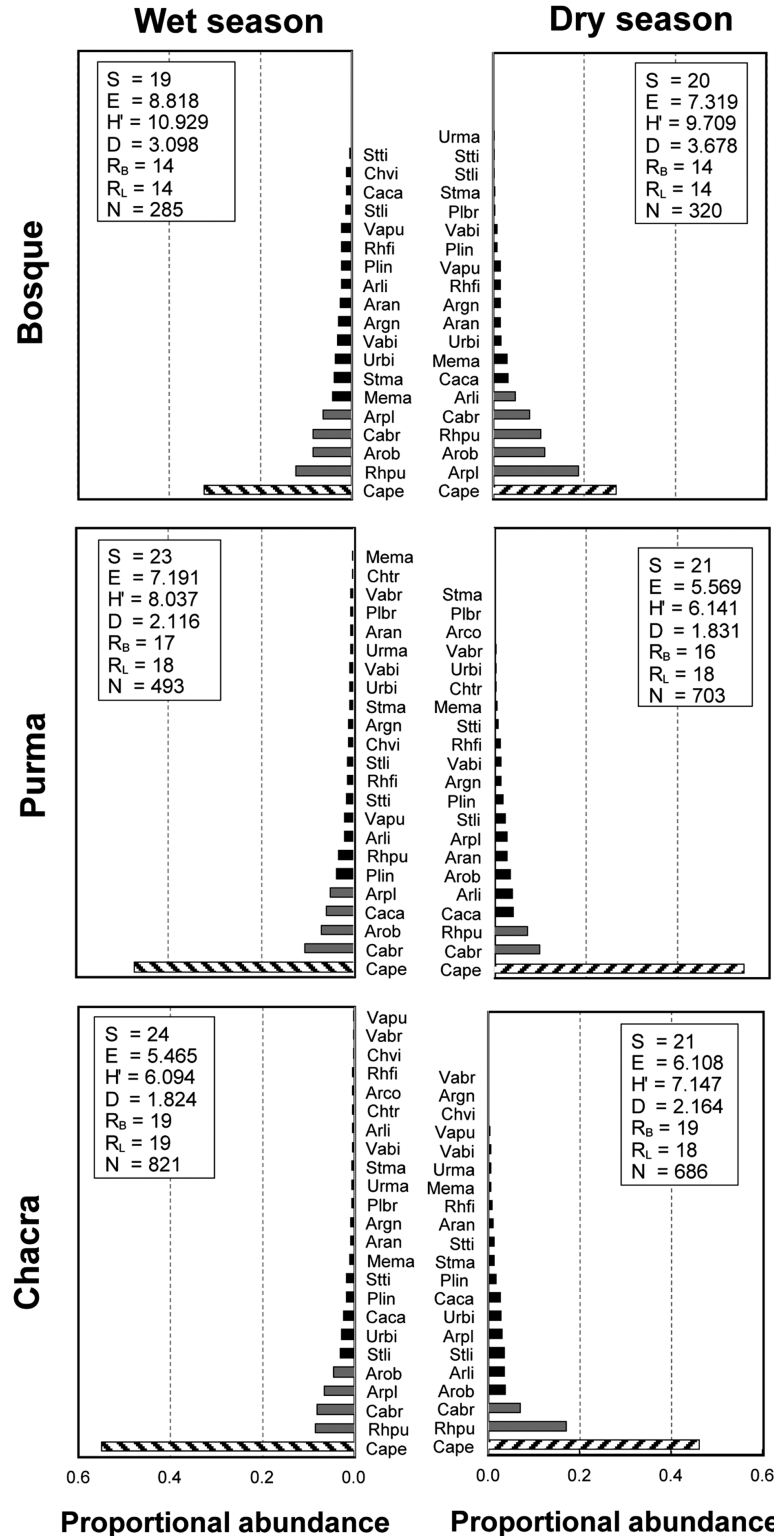


Fig. 3.—Rank abundance distribution (RAD) for frugivores at the γ -level based on proportional abundance for each treatment combination of habitat (bosque, chacra, and purma) and season. For each treatment combination, striped bars represent the dominant species (most abundant), gray bars represent common species (nondominant species with a relative frequency $\geq 1/S$, where S is species richness), and black bars represent rare species (species with a relative frequency $< 1/S$). Species codes appear in Table 1. Metrics of biodiversity (five plots combined per treatment combination) include S , number of species; E , Camargo’s evenness; H' , Shannon diversity; D , Berger–Parker dominance; R_L , local rarity (i.e., number of species with proportional abundance $< 1/S$); R_B , bosque rarity (i.e., number of species with proportional abundance $< 1/S$ based only on relative abundances in bosque); and N , number of individuals. Metrics of biodiversity are reported as numbers equivalents.

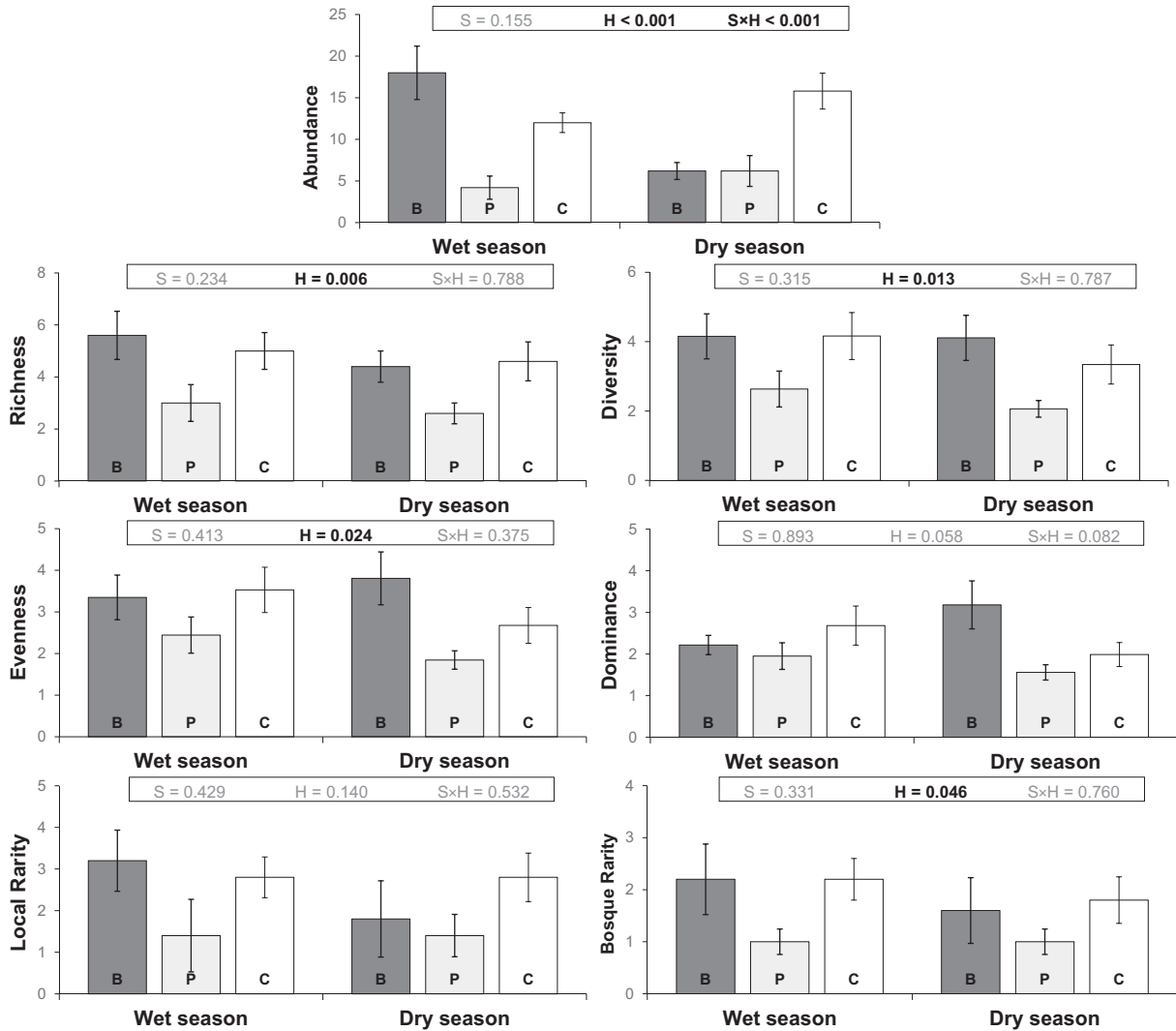


Fig. 4.—Bar diagrams representing mean aspects of gleaning animalivore biodiversity (α -level analyses) for combinations of habitat (B, dark shading, bosque; P, light shading, purma; C, no shading, chacra) and season. *P*-values for treatment effects (S, season; H, habitat; S × H, season by habitat interaction) appear in horizontal frames above bar diagrams, with significance ($P \leq 0.05$) indicated by bold letters and nonsignificance ($P > 0.05$) by gray letters. Although error bars ($\pm 1 SE$) represent measures of dispersion for means within each treatment combination, statistical analyses (GLMMs) were based on repeated measures and do not necessarily reflect the nonoverlap of these error bars. Metrics of biodiversity are reported as numbers equivalents.

Table 3.—Results of chi-square tests comparing species abundance distributions or rank abundance distributions of gleaning animalivores for each combination of season and habitat (γ -level of analysis). Chi-square values are in the lower triangle; *P*-values are in the upper triangle. *P*-values are based on a Monte Carlo simulation using 10,000 iterations. Significant ($P \leq 0.05$) results are in bold.

Season	Habitat	Dry season			Wet season		
		Bosque	Chacra	Purma	Bosque	Chacra	Purma
Species abundance distribution							
Dry	Bosque	—	< 0.001	< 0.001	< 0.001	0.002	0.392
	Chacra	44.1	—	0.002	< 0.001	0.022	0.002
	Purma	28.2	27.1	—	0.027	0.032	0.284
Wet	Bosque	28.9	40.3	19.1	—	0.088	0.261
	Chacra	27.3	21.3	19.2	18.6	—	0.217
	Purma	9.6	28.1	9.5	12.5	13.9	—
Rank abundance distribution							
Dry	Bosque	—	0.085	0.006	0.873	0.844	0.839
	Chacra	14.7	—	0.257	0.399	0.142	0.816
	Purma	18.0	11.0	—	0.309	0.400	0.517
Wet	Bosque	5.8	10.7	11.7	—	0.936	0.919
	Chacra	6.4	14.0	10.5	4.7	—	0.995
	Purma	4.9	5.2	6.8	4.5	2.9	—

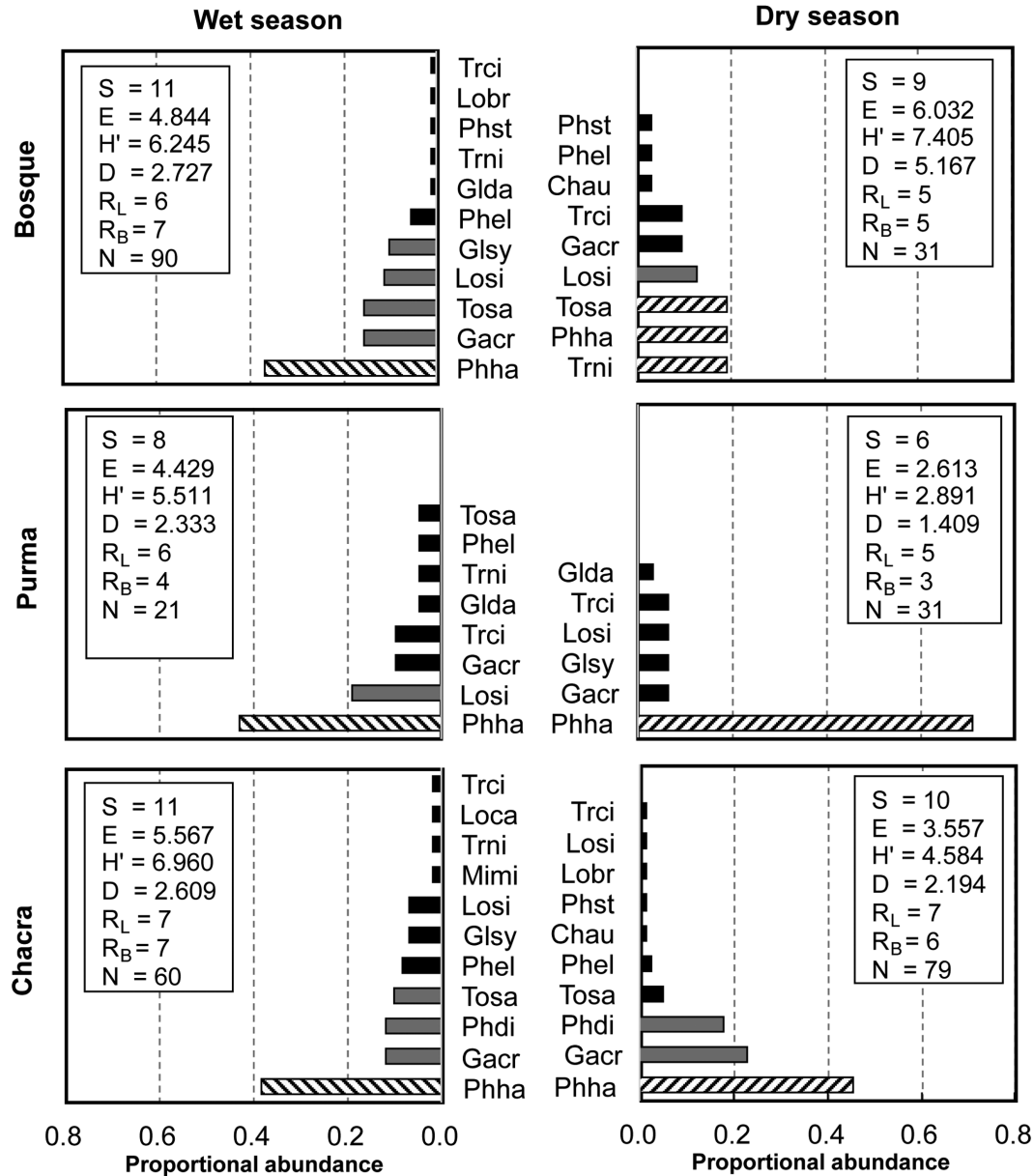


Fig. 5.—Rank abundance distributions (RAD) for gleaning animalivores at the γ -level based on proportional abundance for each treatment combinations of habitat (bosque, chacra, and purma) and season. For each treatment combination, striped bars represent the dominant species (most abundant), gray bars represent common species (nondominant species with a relative frequency $\geq 1/S$, where S is species richness), and black bars represent rare species (species with a relative frequency $< 1/S$). Species codes appear in Table 1. Metrics of biodiversity (five plots combined per treatment combination) include S , number of species; E , Camargo's evenness; H' , Shannon diversity; D , Berger–Parker dominance; R_L , local rarity (i.e., number of species with proportional abundance $< 1/S$); R_B , bosque rarity (i.e., number of species with proportional abundance $< 1/S$ based only on relative abundances in bosque); and N , number of individuals. Metrics of biodiversity are reported as numbers equivalents.

exclusively in bosque. In addition, all but one gleaning animalivore (*Glyphonycteris daviesi*) occupied chacra, all but seven gleaning animalivores (*Chr. auritus*, *Gl. daviesi*, *L. brasiliense*, *L. carrikeri*, *Mic. minuta*, *Phylloderma stenops*, *P. discolor*) occupied purma, and all frugivores occupied both chacra and purma (Table 1). In contrast, three gleaning animalivores (*L. carrikeri*, *Mic. minuta*, *P. discolor*) and three frugivores (*A. concolor*, *Chi. trinitatum*, *V. brocki*) were not recorded from bosque, indicating that these species likely rely on disturbed habitats to maintain populations. Nonetheless, persistence of many bat species in chacra or purma may be predicated, at

least in part, on the proximity of extensive closed-canopy forest (Fig. 1), which harbors source populations that use these habitats. More generally, in the Inambari area, where much of the landscape remains contiguous closed-canopy forest, rescue of local populations from extinction in chacra or purma is likely enhanced via source–sink dynamics (Pulliam 1988; Kelt et al., In press).

Our first prediction received partial support, as bosque had higher diversity and evenness compared to chacra or purma, but purma was not intermediate (Figs. 2 and 4). Our second prediction also received partial support in that *Car. perspicillata*

was more dominant among frugivores in chacra and in purma compared to bosque, but increased dominance among gleaning animalivores did not occur in chacra or purma (Figs. 2–5). Our third prediction, that species composition (SADs) would be distinct for each habitat, was supported during both seasons for frugivores and during the dry season for gleaning animalivores; however, the prediction that the structure of taxonomic biodiversity (RADs) would be distinct for each habitat was not supported for either guild during either season (Tables 2 and 3). Our prediction that gleaning animalivores would be more greatly affected by habitat conversion was not supported: the number of significant responses to habitat conversion was the same for each guild (Figs. 2 and 4), and frugivore species composition (SADs) and structure of biodiversity (RADs) exhibited greater responses than did those of gleaning animalivores (Tables 2 and 3). Finally, our prediction that responses would be greater during the wet season was not supported: only the abundances of gleaning animalivores exhibited a season-specific response, with no metric of biodiversity doing so (Figs. 2 and 4), and species composition and structure of biodiversity exhibited a similar number of differences between habitats during each season, with the exception of species composition of gleaning animalivores (Tables 2 and 3). In general, expectations were not met because bat guilds in purma do not represent intermediate versions of those in chacra and bosque, and because stronger responses were not manifest by the guild we expected to be more sensitive to habitat conversion (gleaning animalivores) or during times of high resource abundance (wet season) that would allow species to restrict their activities to more desirable habitats.

Conversion of Forest to Agriculture

Species composition.—Effects of conversion of bosque to chacra on species composition were guild-specific. For frugivores, species composition of chacra differed from that of bosque regardless of season (Table 2; Supplementary Data SD5). The relative abundance of *Car. perspicillata*, the most dominant species in the environs of Iquitos, was 50% greater in chacra than in bosque. In contrast, the relative abundance of the four common and all rare species did not appreciably differ between bosque and chacra. For gleaning animalivores, species composition of chacra differed from that of bosque only in the dry season (Table 3; Supplementary Data SD6). During that season, three species (i.e., *Trinycteris nicefori*, *Phyllostomus hastatus*, and *Tonatia saurophila*) were co-dominant in bosque. In chacra, two of these species (i.e., *Tr. nicefori*, and *To. saurophila*) were rare, and one (*P. hastatus*) more than doubled in relative abundance. Moreover, the common species in bosque during the dry season (i.e., *Gl. sylvestris*) was rare in chacra during that season. In contrast, two rare species in bosque during the dry season (i.e., *Gardnerycteris crenulatum* and *P. discolor*) were common in chacra, even though mean bosque rarity in chacra and bosque were indistinguishable (Supplementary Data SD4). Thus, even if species persist in agricultural lands, their likelihood of interaction with other species in their guild, as well as their contributions to ecosystem function, may have

differed greatly at the local scale (i.e., at the plot or treatment level), where the identity and abundances of species were quite distinctive from that in closed-canopy forest.

Bats were more abundant in chacra (1,737 total captures) and in purma (1,290 captures) than in bosque (737 captures); this was driven primarily by increases in the abundances of frugivorous and nectarivorous bats (Willig et al. 2007; Fig. 2). Because chacras are typically created near human habitations, the greater abundances of bats in chacra and purma may represent increased risk of transmission of diseases to humans, especially diseases carried by species (e.g., *Car. perspicillata*) that exhibit dramatic responses to these human activities. Although outbreaks of zoonoses related to hyperabundant mammalian vectors or reservoirs have not been reported for disturbed habitats of the Iquitos region, zoonoses have been recorded from *Car. perspicillata* in the Neotropics, including *Bartonella* spp. in Costa Rica (Judson et al. 2015) and Guatemala (Bai et al. 2011), rabies in Brazil (Fernandes de Almeida et al. 2011), coronaviruses in Mexico (Anthony et al. 2013), *Leishmania chagasi* in Venezuela (De Lima et al. 2008), and *Trypanosoma* spp. (including *T. cruzi*) in Colombia (Ramírez et al. 2014). Moreover, zoonotic outbreaks have occurred in other regions in similar circumstances. For example, habitat conversion in the United States has increased risk of Lyme disease for humans due to increased abundances of its most competent reservoir (*Peromyscus leucopus*—Allan et al. 2003). Similarly, habitat loss in rural regions of Bangladesh has resulted in more bats roosting in buildings of small villages. This increase in proximity of bats and humans has led to outbreaks of Nipah virus, which is transmitted by the bats, in those rural human populations (Hahn et al. 2014).

Ecological structure.—The identity of species is irrelevant in the construction of RADs or in the calculation of metrics of taxonomic biodiversity; thus, both provide taxon-free delineations of ecological structure that facilitate intergroup comparisons (e.g., comparisons of treatment combinations), even when no species are shared between groups. Moreover, many metrics of taxonomic biodiversity (e.g., species richness, evenness, dominance, diversity, and rarity) can be conceptualized as univariate parameters that characterize the shape of RADs (Supplementary Data SD3).

For frugivores, RADs differed between bosque and chacra in both seasons (Table 2; Fig. 3). For the most part, this difference occurred because of the higher relative abundance of the dominant species in chacra compared to bosque, and the slight reduction in relative abundances of most other species ranks. At the scale of plots, these differences manifested as greater mean abundance, dominance (lower hill number), and local rarity in chacra compared to bosque (Fig. 2; Supplementary Data SD4). Moreover, at the γ -level (treatment combinations; Fig. 3), chacra supported greater bosque rarity (i.e., $R_{B\text{ wet}} = 19$; $R_{B\text{ dry}} = 19$) than did bosque itself (i.e., $R_{B\text{ wet}} = 14$; $R_{B\text{ dry}} = 14$).

For gleaning animalivores, RADs did not differ between bosque and chacra during either season (Table 2; Fig. 5). Similarly, no metrics of biodiversity differed between bosque and chacra at the α -level (Supplementary Data SD4).

Nonetheless, mean abundance in chacra differed from that in bosque in a season-specific manner: mean abundance in chacra was lower during the wet season and higher during the dry season compared to contemporaneous mean abundances in bosque (Supplementary Data SD4; Fig. 4).

Although most species of frugivore or gleaning animalivore frequent or obtain resources from chacra, guild composition in terms of species identity and ecological structure were distinctive in chacra compared to those in bosque at the α - and γ -levels for frugivores, but not for gleaning animalivores. The primary response by frugivores to chacra was for dominance to be higher than in bosque, with the same dominant species (*Car. perspicillata*) in both habitats. Such dynamics did not characterize gleaning animalivores.

Conservation Value of Successional Forest

Species composition.—Purma and bosque harbored similar suites of frugivorous species (Table 1) during the wet season (19 of 19 species) and during the dry season (18 of 20 species). Nonetheless, frugivorous species composition of purma, which considers relative abundance rather than only incidence of species, was distinguishable from that of bosque during both seasons (Table 2; Supplementary Data SD5). This was primarily a consequence of higher abundance of *Car. perspicillata* and lower abundance of *R. pumilio* in purma than in bosque.

The situation was different for gleaning animalivores. Purma harbored only a modest subset of the species from bosque during each season (four of nine in the dry season; seven of 11 in the wet season). Nonetheless, a difference between the two habitat types in species composition was evident only in the dry season (Table 3), and was primarily driven by the much higher abundance of *P. hastatus* in purma than in bosque.

Ecological structure.—For the frugivore guild, differences in RADs between bosque and purma depended on season (i.e., no difference in wet season, significant difference in dry season), and were strongly related to variation in abundance of the most dominant species, *Car. perspicillata*. This was reflected in metrics of taxonomic biodiversity at the γ -level (Fig. 3), where differences (Δ) between purma and bosque were greater during the dry season ($\Delta E = 1.7$, $\Delta H' = 3.6$, $\Delta D = 1.8$) than during the wet season ($\Delta E = 1.6$, $\Delta H' = 2.9$, $\Delta D = 1.0$). At the α -level, metrics of taxonomic biodiversity differed between purma and bosque as well. More specifically, mean abundance was greater in purma than in bosque, with the former evincing lower mean diversity, lower mean evenness, and higher mean dominance.

For the gleaning animalivore guild, RADs differed between bosque and purma during the dry but not the wet season (Table 3). This was primarily due to a large difference in the relative abundance of the dominant species (0.7 in purma versus 0.2 in bosque) and appreciable differences in the relative abundances of species ranked two (< 0.1 in purma, 0.2 in bosque) and three (< 0.1 in purma, and 0.2 in bosque). At the γ -level (Fig. 5), metrics of mean taxonomic biodiversity evince a similar pattern: differences between purma and bosque were much greater in the dry season ($\Delta E = 4.8$, $\Delta H' = 4.5$, $\Delta D = 3.8$) than in the wet season ($\Delta E = 0.4$, $\Delta H' = 0.7$, $\Delta D = 0.4$).

Implications and Synthesis

Understanding the responses of Neotropical bats to the conversion of forest to agriculture and the subsequent emergence of secondary forest after agricultural abandonment is critical for guiding management and policy in the Anthropocene. This is true because bats constitute an appreciable portion of mammalian diversity in the Neotropics (Kaufman 1995; Meserve 2007), are locally abundant throughout much of the Neotropics, and contribute significantly to multiple ecosystem functions, such as seed dispersal, flower pollination, and arthropod control (Muscarella and Fleming 2007; Novoa et al. 2011; Maas et al. 2016; Williams-Guillen et al. 2016), which ultimately enhance ecosystem services. Moreover, forest regeneration resulting in greater amounts of secondary forest is among the most dominant forms of land use change in the tropics (Asner et al. 2009; Dent and Wright 2009). Nonetheless, considerable variability at the population-, guild-, and assemblage-level characterizes the responses of bats to agriculture and successional forests (Avila-Cabadilla et al. 2012; Meyer et al. 2016). In part, that variability is likely related to the different landscape contexts (e.g., forest area, composition, and configuration) in which conversion and succession occur, as well as to the nature and history of the dominant agricultural practices in the area.

In locations where extensive closed-canopy forest persists, small-scale agriculture (e.g., chacras), especially when associated with secondary forest patches (purma), may not negatively affect species richness for frugivores or gleaning animalivores at larger spatial scales, and may in fact support species in both guilds that are rare in large contiguous closed-canopy forests. The extent to which this is true would likely diminish as total area of closed-canopy forest decreases, the extent to which abandonment of agricultural plots and secondary succession are reduced and impaired, respectively, and the intensity of and total area devoted to agriculture increases. Nonetheless, it is clear that even in areas with limited habitat conversion and fragmentation, species composition and some aspects of taxonomic biodiversity (e.g., evenness, diversity, dominance) do change significantly in response to agricultural conversion and remain statistically different from closed-canopy forest, even in successional forest. Thus, the effective contribution of bats to ecosystem function may change to the extent that the frequency and intensity of species interactions in the mosaic of habitats in an area are related to abundance-weighted aspects of biodiversity. The consequences of such changes to ecosystem services remain an important challenge that should receive higher priority in conservation action (Lacher et al., In press). Indeed, the optimal composition and configuration of habitats in “working landscapes” or ones with mixed use, including land uses dominated by human activities, should receive increasing attention in a world where socioecological systems are becoming the norm (Chazdon 2014).

Finally, bats are hosts for a wide range of microorganisms, especially viruses, some of which are important human pathogens such as filoviruses (Olival and Hayman 2014), coronaviruses (Menachery et al. 2017), and hepadnaviruses (Nie et al. 2018). From 2007 to 2013 alone, 248 novel viruses

belonging to 24 viral families were described from bats, and the Neotropics have been under sampled compared to other tropical regions (Young and Olival 2016). The abundance and diversity of hosts that serve as reservoirs or vectors of disease can influence human exposure to zoonotic pathogens through the “dilution effect,” especially when the most competent host(s) persist or increase in abundance following declines in biodiversity (Johnson et al. 2015). Thus, the effects of deforestation on bat populations and communities could have major impacts on the emergence and circulation of infectious diseases.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Aspect photos of the three habitat types from which bats were obtained in the vicinity of Iquitos, Perú. A) Contrast of overall habitat stature, with a recently cleared and planted chacra in the foreground, adjacent purma (secondary growth) in the midground, and closed-canopy forest (bosque) in the background. B) Typical 3-year-old chacra planted with a mixture of plantains, manioc, and pineapple. C) Characteristic dense growth of young trees in purma, with most woody vegetation < 10 cm dbh and < 10 m tall. D) Bosque, which generally has a more open and shaded understory than does purma, and a canopy of large trees that are > 30 m tall. Modified from Willig et al. (2007); photographs courtesy of S. Yanoviak.

Supplementary Data SD2.—Each sampling plot comprised four interior and four exterior subplots within which mist nets were erected to sample bats from bosque, chacra, and purma habitats near Iquitos, Peru (see text for details). Schematic

diagram is drawn to scale, with each interior subplot measuring 75 m × 75 m.

Supplementary Data SD3.—Graphical representation of a hypothetical rank abundance distribution (RAD). In general, many metrics of taxonomic biodiversity (e.g., species richness, evenness, dominance, diversity and rarity) are characterizations of the shape of the distribution. The yellow shaded area identifies the threshold for relative abundance (< 1/S, where S is species richness) below which a species is considered rare. The blue bar corresponds to the most abundant species, and its height represents Berger–Parker dominance. The light red bars represent species that are rare, and the horizontal red line represents rarity (the number of rare species). The white bars represent common species (i.e., those whose relative abundance is > 1/S, excluding the dominant species). A maximally even community will be one in which the relative abundances all species correspond to the height of the yellow shaded area. Deviations from perfect evenness are represented by vertical green arrows. Diversity captures the overall shape of the curve and comprises richness and evenness.

Supplementary Data SD4.—Post hoc pairwise comparisons of means among habitat types for each general linear mixed-effects model (GLMM) that exhibited a significant (*) effect of habitat (H) or a habitat by season interaction (H × S) on abundance or biodiversity. Comparisons of habitats were conducted separately for each season in the case of a H × S interaction. Post hoc comparisons were not conducted for analyses that returned nonsignificant results (NS). Analyses were conducted using a Tukey test with a Holm–Šídák adjustment for P-values. Analyses were conducted in R 3.2.2 using the `glht` function from the `multcomp` library (Hothorn et al. 2008). Comparisons that were significant ($P \leq 0.05$) or approached significance ($0.10 > P \geq 0.05$) are bold, indicating contrasts that most contributed to overall differences between habitats.

Supplementary Data SD5.—Species abundance distributions for frugivores at the γ -level based on their proportional abundances for each treatment combination of habitat (bosque, chacra, and purma) and season. For each treatment combination, striped bars represent the dominant species (most abundant), gray bars represent common species (nondominant species with a relative frequency $\geq 1/S$, where S is species richness), and black bars represent rare species (species with a relative frequency < 1/S). Species are listed in alphabetical order based on scientific name; species codes appear in Table 1. If a species is not present in a particular treatment combination, its species code appears in gray letters.

Supplementary Data SD6.—Species abundance distributions for gleaning animalivores at the γ -level based on their proportional abundances for each treatment combination of habitat (bosque, chacra, and purma) and season. For each treatment combination, striped bars represent the dominant species (most abundant), gray bars represent common species (nondominant species with a relative frequency $\geq 1/S$, where S is species richness), and black bars represent rare species (species with a relative frequency < 1/S). Species are listed in alphabetical order based on scientific name; species codes appear in Table 1. If a

species is not present in a particular treatment combination, its species code appears in gray letters.

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