

Climate, habitat, and species interactions at different scales determine the structure of a Neotropical bat community

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Abstract. Climate, habitat, and species interactions are factors that control community properties (e.g., species richness, abundance) across various spatial scales. Usually, researchers study how a few properties are affected by one factor in isolation and at one scale. Hence, there are few multi-scale studies testing how multiple controlling factors simultaneously affect community properties at different scales. We ask whether climate, habitat structure, or insect resources at each of three spatial scales explains most of the variation in six community properties and which theory best explains the distribution of selected community properties across a rainfall gradient. We studied a Neotropical insectivorous bat ensemble in the Isthmus of Panama with acoustic monitoring techniques. Using climatological data, habitat surveys, and insect captures in a hierarchical sampling design we determined how much variation of the community properties was explained by the three factors employing two approaches for variance partitioning. Our results revealed that most of the variation in species richness, total abundance, and feeding activity occurred at the smallest spatial scale and was explained by habitat structure. In contrast, climate at large scales explained most of the variation in individual species' abundances. Although each species had an idiosyncratic response to the gradient, species richness peaked at intermediate levels of precipitation, whereas total abundance was very similar across sites, suggesting density compensation. All community properties responded in a different manner to the factor and scale under consideration.

Key words: *acoustic monitoring; community composition and structure; Emballonuridae; emergent properties; insectivorous bats; Mormoopidae; Neotropics; Panama; rainfall gradient; spatial scale; variance partitioning; Vespertilionidae.*

INTRODUCTION

One of the central themes in community ecology is to understand what factors determine community structure and at which spatial scale these factors control species composition and diversity (Wiens 1989). Among the factors proposed, climate, habitat, and species interactions appear to play the most important roles (McGill 2010). First, climate controls species distributions and local abundances by producing, for example, physiological stress (Root 1988). Second, habitats provide limiting resources, they aggregate the microclimatic conditions that limit species survival and they set the stage for species interactions (Wiens 1989). As an example, they provide shelter from predators and food resources. In turn, species interactions, either negative or positive, modify species distributions by association, exclusion, or

consumption, leading to shifts in species composition and distribution (MacArthur 1965).

These three factors are thought to affect community structure in a scale-dependent fashion. Climate influences communities at very large scales, whereas habitat effects are likely more restricted to smaller scales. Finally, species interactions may usually influence richness and abundance at a scale determined by the movement patterns or home ranges of the individuals. Although these factors are known to exert strong influence on abundance and composition (Boone and Krohn 2000, McCain 2007, Meynard and Quinn 2008, Jung and Kalko 2010, Qian and Kissling 2010), few studies have explicitly tried to separate the effect of each factor on different community properties (e.g., richness, abundance) and to assess at which scales they operate.

Variation of climatic conditions such as rainfall across space creates an environmental gradient. Such gradients are known to affect community structure and composition (Rosenzweig 1995). They can do so by producing varying amounts of physiological stress from one end to the other end of the gradient and/or by affecting vegetation structure and composition. However, the

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distribution of these effects is not the same in all cases. For example, plant and animal communities may respond in a different way to rainfall gradients (Mittelbach et al. 2001). Diversity can have a linear, a uni-modal distribution, or show no relationship with increasing rainfall and productivity (Whittaker 2010). For example, the richness of Neotropical trees levels out at very high levels of rainfall (Gentry 1988), whereas the incidence of leaf miners does not seem to be influenced by rainfall gradients (Sinclair and Hughes 2008) and the richness of African herbivorous mammals peaks at intermediate rainfall (Rosenzweig 1995).

Several hypotheses have been proposed to explain these patterns. The “environmental heterogeneity” hypothesis predicts that diversity increases with rainfall. However, after a certain level, habitats tend to be more homogeneous because micronutrient heterogeneity in space drops, which then lowers habitat heterogeneity. As one of the main consequences, animal diversity decreases (Rosenzweig 1995). Other hypotheses predict that disturbances at small scales or changes in the competitive structure might lead to higher diversity at intermediate levels of rainfall (Whittaker et al. 2001). Yet, there is still a lack of consensus regarding the effect of rainfall gradients on community properties aside from richness. Thus, it is crucial to move beyond a mere description of how rainfall affects a single community property, such as richness, and to assess how environmental gradients at several spatial scales might impact community structuring while explicitly incorporating controlling factors such as climate, habitat, and species interactions (McGill et al. 2006).

Neotropical bats are an ideal model group for studying community patterns and their underlying processes (Kalko 1998, Stevens et al. 2007). The ensemble of aerial insectivorous bats that is composed of hawking species that depend on echolocation to navigate, orient, and hunt prey (Schnitzler and Kalko 2001) forms a very diverse group. As an example, almost half (46%) of the species of the entire bat assemblage on Barro Colorado Island (BCI; $N = 74$ bat species), Panama, belong to this group (Kalko et al. 2008). Despite the high diversity and crucial role of insectivorous bats as control agents of insects (Cleveland et al. 2006, Kalko et al. 2008), information about this ensemble in Neotropical rainforests is still scarce (MacSwiney et al. 2008, Jung and Kalko 2010).

Bats, and in particular, the insectivorous ensemble, are well suited for investigating how different community properties are influenced by climate, habitat, and species interactions at various spatial scales (Fahr and Kalko 2010). First, climate may affect species spatial distributions and abundances at large scales because bats are sensitive to temperature and humidity due to their small size and high surface-to-volume ratio (Hosken and Withers 1999, Ruggiero and Kitzberger 2004, McCain 2007). Second, the structural complexity of the habitat, at the scale of a forest patch, imposes

ecomorphological constraints on bat mobility, in terms of wing shape, and requires specific sensorial adaptations for finding food. These constraints limit the type and number of species that are able to navigate and successfully forage in different habitat types (Norberg and Rayner 1987, Schnitzler and Kalko 2001). Third, bats, as well as any other kind of co-existing species, are likely to be limited by resources, in our case availability of insects. However, there are conflicting hypotheses whether food is always a limiting resource. On the one hand, Fenton (1990) suggested that there is little evidence of food limitation for aerial insectivorous bats. On the other hand, Morris et al. (2010) found that insect availability affected both ensemble and species specific relative abundances of aerial insectivorous bats.

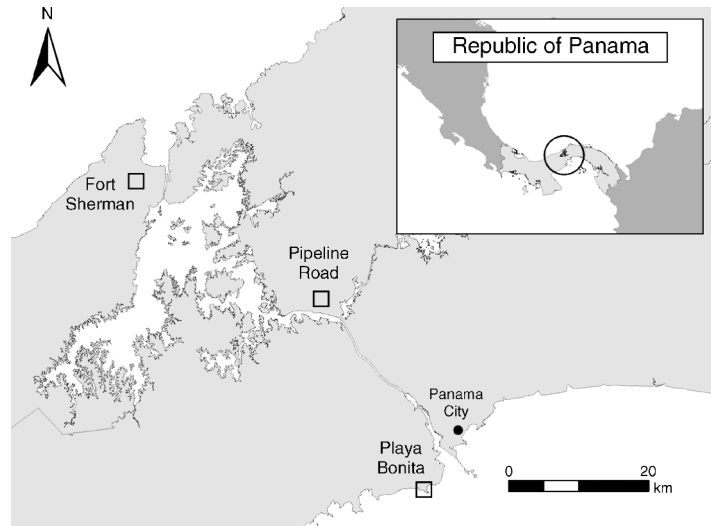
Taking the diverse factors into account and the conflicting views on resource limitation, we studied aerial insectivorous bats across a rainfall gradient in the Isthmus of Panama and hypothesized that they should be affected by climate, habitat structure, and insect resources at different spatial scales, both at the ensemble and the species level. In particular, we predicted that (1) community properties would be mostly explained by climate and habitat structure and less by insect resources (Fenton 1990, Lopez-Gonzalez 2004, Jung and Kalko 2010). We also expected that (2) larger scales would primarily influence species distributions, in terms of their abundances, whereas species richness would be affected at smaller scales (Wiens 1989). Finally we anticipated that (3) community properties should show a hump-shaped response to the rainfall gradient given the results of Mittelbach et al. (2001) on animals at the landscape scale and the reanalysis of Whittaker (2010) with a refined data set and a more circumspect analysis.

METHODS

Study area

Our study was conducted at three sites on the Isthmus of Panama: Fort Sherman (now San Lorenzo National Park) on the Caribbean side, Soberanía National Park (hereafter Pipeline Road) in the center of the isthmus, and Playa Bonita, a private reserve on the Pacific side about 8 km southwest of Panama City (Fig. 1). Climate along the canal is strongly seasonal, with a rainy season from April to December and a marked dry season during the rest of the year (Windsor 1990). Total precipitation declines from 3020 mm per year on the Caribbean side to 1600 mm on the Pacific side of the isthmus. Concomitantly, the number of dry days (i.e., when rainfall is less than the mean monthly evapotranspiration) in the Pacific side is higher (129 days) compared to the Caribbean side (102 days) (Condit 1998). This climatic gradient produces a shift in life zones ranging from a lowland tropical wet forest at the Caribbean side (Fort Sherman) to a semi-deciduous, lowland tropical moist forest in Pipeline Road toward a dry tropical forest next to the Pacific (Playa Bonita) (Holdridge 1967) across a small distance <100 km

FIG. 1. Map of the study area across the Isthmus of Panama in Central Panama (inset). Study sites are enclosed in boxes: Fort Sherman (wet Caribbean side), Pipeline Road (middle), and Playa Bonita (dry Pacific side).



between the outermost sampling points. Human intervention increases with increasing proximity to the Pacific coast (Condit et al. 2001). However, as the Panama Canal watershed has been protected since the 1920s, the status of the forest along the canal has been relatively contiguous for at least 90 years because most areas were and are protected from logging by Panamanian law (S. Heckadon, *personal communication*).

Sampling design

We determined species richness, composition, and relative abundance of aerial insectivorous bats using acoustic surveys. At each study site, acoustic surveys were conducted along five linear transects (200 m) each with seven recording stations (30 m apart). The location and direction of each transect was chosen randomly with a minimum distance of 150 m. To ensure accessibility, no transect was more than 400 m away from the next. Roads, trails, old construction sites, or steep terrain ($>45^\circ$) were avoided.

Sound recordings and analysis

We visited each transect three times between November 2008 and August 2009 in order to include compositional variation related to seasonal differences. Each visit consisted of four 1-h walks along each transect beginning at sunset. The four walks per visit were intended to account for fluctuations in species-specific abundances during the first hours of the night. We limited our recordings to a fixed time period of four hours (18:00–22:00) to ensure comparability between recording sites. Furthermore, activity of aerial insectivores decreased considerably after 22:00 hours. Usually, most aerial insectivorous species present in an area can be documented reliably with acoustic methods during this time period (E. Kalko and K. Jung, *personal observations*; K. Jung, *personal communication*). Rainy nights were avoided. Each recording station was surveyed for 5 min, and all bats that were detected were

recorded on a real time high-speed recording unit (UltraSoundGate 116, Avisoft-recorder, Avisoft Bioacoustics, Berlin, Germany; see details in Appendix A). The total recording time per site was 34.95 hours, with 104.85 hours for the whole study period. Analysis of sound sequences was accomplished with Avisoft SASLAB PRO software (version 4.34; Specht 2005) following the methods and settings described in Estrada-Villegas et al. (2010). We defined a bat pass as a regular succession of sound pulses emitted by a bat flying on-axis towards the microphone (Fenton 2004). Feeding activity was measured by registering feeding attempts (i.e., feeding buzzes, a rapid succession of echolocation calls prior to a capture attempt) for each species (Schnitzler and Kalko 2001). Species identification was achieved by measuring different call parameters on the computer screen (for parameters see Table 2 in Estrada-Villegas et al. 2010). Faint recordings where signal energy did not exceed background noise by -10 dB or more were excluded from analysis (19.6% of 9033 recordings). We used the echolocation call library of the species known to occur in the Barro Colorado Nature Monument (E. Kalko, *unpublished data*) for reference. Other identification parameters for species that are difficult to identify can be found in Appendix A.

Vegetation data

A 10×10 m plot was located around each recording station, and six vegetation variables were recorded. The total number of trees (diameter at breast height [dbh] >10 cm) and the number of *understory* saplings and shrubs (>2.5 and <10 cm dbh) were counted and measured (variables used in the analysis are shown in *italic* at the first use). Lianas and palm stands were included because they increase the amount of obstacles bats have to detect and evade while flying. *Basal area* was then calculated for each plot pooling all the dbh data. *Canopy height* was measured at the center of the plot with a range finder (Leica Geosystems, Heerbrugg,

Switzerland), and a measure of vertical *foliage structure* was taken directly above the recording station by noting the presence or absence of foliage at 11 different height intervals (0–1, 1–2, 2–4, 4–8, 8–12, 12–16, 16–20, 20–24, 24–28, 28–32, >32 m). *Canopy openness* was measured by taking a full-frame hemispherical photograph (Nikon D3 camera, Nikkor AF 16mm f/2.8 D Fisheye lens; Nikon, Tokyo, Japan) and calculating the percentage of white pixels (Engelbrecht and Herz 2001). Finally, the presences of *forest gaps* (sensu Schemske and Brokaw 1981) and *streams* with permanent courses were noted if next to or within 5 m of the plot.

Insect data

We sampled insects at the transect level using three passive omnidirectional flight interception traps positioned at different heights (>10 m, >5 m, 1 m). Insects were collected for the same time interval as the bat recording sessions (18:00–22:00) for all transects and sites; tallying to a total of 180 hours of trapping time per site per trap. We identified and counted all insects up to order level (Coleoptera, Hemiptera, Orthoptera, Diptera, Hymenoptera, Blatodea, Ephemeroptera). Other rare orders or unknown samples were grouped in one category. Samples were oven-dried at 60°C for 24 h and weighed on a scale to the nearest 0.0001 g. We derived three variables: *insect abundance* (total amount of insects that were trapped), *richness* (total number of insect orders, maximum = 8), and *biomass* (dry mass).

Climatic data

Climate data were collected for each of the three sites. Monthly *temperature*, *rainfall*, and *wind speed* data were obtained from two sources; the Smithsonian Tropical Research Institute weather station in Fort Sherman and two additional weather stations (Gamboa and Panama Balboa Heights) from the Autoridad Canal de Panamá (*available online*).⁶ Weather stations were within 8.5 km radius from our working sites. Data were recorded for all years between 1998 to 2005 or 2006. We used a multiyear data set so the year-to-year variations could be incorporated in the analysis. We selected only the months when we visited each transect and calculated a monthly average across all years. This monthly average was then assigned to the corresponding month when we visited each transect. Despite the fact that rainfall and wind speed can be very local and data were not collected at each transect, we are convinced that eight years of data are representative for the trend of climatic conditions at this scale of analysis.

Data analysis

Given that successive bat passes can potentially be from the same individual, comparisons of composition among sites are complicated because passes represent an

index of activity rather than a true count of individuals. Therefore, to ensure that individual-based analyses can be applied and the effects of serial autocorrelation are minimized, we generated an abundance index by counting once the occurrence of a particular species in each 5-min recording time at each recording station. Based on our observations, we are confident in assuming that these counts were different individuals because of the long time interval between each walk per visit and between visits. We then pooled the occurrences across all visits per recording station and subsequently used the count data (hereafter abundance index) for all statistical comparisons (Estrada-Villegas et al. 2010).

Community properties.—To represent community structure, we used seven community properties as response variables in the analyses. These were: total number of bat species recorded per recording station (*S*); total abundance index, which represents the sum of abundance index from all species per recording station (*N*); total feeding attempts which consists of the sum of feeding attempts (terminal buzzes) of all species per recording station (*F*); and abundance index per species, a multivariate response variable in a matrix form (*SC*), recording stations in rows, bat species in columns, and count data in cells. *SC* denotes the species composition per recording station. Finally, we performed a principal component analysis to create three univariate measures of community structure (PCA1–3).

To calculate the principal component analysis we used the abundance index per species (i.e., the same *SC* matrix) as input and the first three ordination axes (PCA1–3) as output because they represented most of the observed variation in community composition (>75% of total variation). Moreover, these three axes captured the contribution of the most abundant species in terms of their loadings in each ordination axes. We used the scores of PCA1–3 to compare each axes with any explanatory variable because they retain the order of the recording stations. The seven community properties, which are response variables, can be placed conceptually into two groups: emergent properties (*S*, *N*, and *F*), which refer to all univariate measures of community structure; and community composition (*SC* and PCA1–3), which encompass the multivariate measures of community composition (i.e., details of species presences).

Scale and community properties.—To test our predictions that emergent properties would be differentially affected by spatial scale, we established three scales relevant for both the extent of the isthmus and the organisms under study. The recording station and its surrounding plot represented the smallest scale and reflected the patch where bats fly and forage (Bradbury and Vehrencamp 1976). The respective transect represented the intermediate scale and reflected the array of patch heterogeneity within a habitat that an organism would experience in its foraging area (Hoffmann et al. 2007). Sites represented the largest scale and reflected

⁶ <http://biogeodb.stri.si.edu>

the forest life zones across the isthmus, which in turn are strongly defined by climate (Holdridge 1967). We are aware that the largest scale did not have spatial replications compared to the plots and transects. However, we ensured that each site where we worked at was representative of the respective life zone. Furthermore, all sites were similar in forest structure and composition to those studied by Condit (1998). Moreover, we could not conduct spatial replication at this scale due to logistical reasons and because other potential sites on the dry side of the gradient were highly deteriorated by urban encroachment (S. Estrada-Villagas, *personal observations*).

To determine the amount of variation explained by each scale, we partitioned the variances of the emergent properties (i.e., response variables) with site, transect, and plot as explanatory variables. Following the methods of McGill (2008), we first fitted a minimal adequate linear mixed-effects model (LMM) determining the nested hierarchy of scales as random effects on the community properties, as with a nested ANOVA, and then used the function “varcomp” within the “ape” package in R (Paradis et al. 2004) to determine how much variation each scale explained.

Factors and community properties.—In order to test our predictions, we considered 15 variables to determine how much variation of the emergent properties and community composition was explained by climate, habitat structure, and insect resources. These 15 variables, in turn, were grouped into three broad categories and used as explanatory variables: habitat structure (HS), resources or insects (IN), and climate (C). We refer to these three explanatory variables as “controlling factors,” since they are the candidates for determining community structure. These three controlling factors group the 15 variables as follows: (1) effects of habitat structure not explained by food resources or climate (HS), including number of trees, understory, basal area, canopy height, foliage structure, canopy openness, forest gaps, and streams; (2) effects of insect resources are not explained by other factors (IN), including insect abundance, richness, and biomass; and (3) effects of climate not explained by other factors (C), and groups temperature, rainfall, and wind.

We also explored four combinations of the three broad categories (HS+IN, HS+C, IN+C, HS+IN+C). Prior to determining the amount of variation explained, we calculated a Pearson correlation matrix with all 15 variables to avoid including variables that were excessively collinear. We used an arbitrary, but commonly used cutoff of correlation higher than 0.8, eliminating one of each pair above this threshold. Then we performed multivariate partitioning of variance to determine how much variation (adjusted R^2) in the emergent properties and community composition can be explained by each of the three controlling factors and combinations thereof. Any unexplained variance in our analysis was labeled UNEXP.

Multivariate partitioning of variance is a powerful tool to simultaneously tease apart the effect of several explanatory variables that are not mutually exclusive. Therefore, it allowed us to consider the relative contribution of each controlling factor on community structure while accounting for the simultaneous variation of other controlling factors (Legendre and Legendre 1998). For this analysis we used an extension of the methods developed by Borcard et al. (1992) incorporated in the function “varpart” within the “vegan” package for R (Oksanen et al. 2009). To test for differences in total abundance index (N) and total feeding attempts (F) along the climatic gradient (among sites), we employed a generalized LMM, using sites as fixed effects and recording stations nested within transects as random blocking effects. We compared N among sites and abundance index per species among sites with a Poisson GLMM using function `lmer` in the “lme4” package in R (Bates and Meachler 2010). For F and feeding attempts per species, Gaussian LMMs were fitted using the “nlme” package in R (Pinheiro et al. 2009), following $\log(x+1)$ transformation. To assess whether N , F , abundance index per species, and feeding attempts per species differed among sites, we conducted multiple comparison tests using Tukey contrasts as implemented in the “multcomp” package in R (Hothorn et al. 2008). For species-level analyses, we only used those species with an abundance index greater than 70 because we considered that a lower abundance index would represent species not adequately sampled. We contrasted species richness (S) among sites using rarefaction techniques implemented in the program `EcoSim` (Gotelli and Entsminger 2001). Predictions were made at a standard number of abundance index for all sites and compared with 95% confidence intervals against Pipeline Road, the site with the lowest abundance.

Finally, to determine bat inventory completeness, we calculated randomized (1000 \times) sample-based species accumulation curves for each recording station. Curves were then rescaled to number of individuals to allow for direct comparison of species richness (Gotelli and Colwell 2001). We then calculated expected species richness, S_{est} , using the Michaelis-Menten richness estimator given that it was the most suitable estimator based on the type of organisms we studied (Brose and Martinez 2004). Then, completeness was calculated as observed species richness (S_{obs})/estimated species richness (S_{est}) \times 100. Species accumulation curves and estimators were calculated with the program `EstimateS` 8.2 (Colwell 2005).

RESULTS

We recorded 6280 bat passes for a total abundance index of $N = 1700$ belonging to 14 species. The family Emballonuridae had the most species ($S = 7$), followed by Vespertilionidae ($S = 4$) and Mormoopidae ($S = 3$) (Appendix B). *Saccopteryx bilineata* (Emballonuridae)

TABLE 1. Total abundance index (N), total feeding attempts (F), rarefied species richness, number of species, and survey completeness among sites across the Isthmus of Panama.

| Site | Position on isthmus | N (mean \pm SD) | F (mean \pm SD) | Rarefaction (low and high 95% CI) | S_{obs} | S_{est} | Completeness (%) |
|---------------|---------------------|---------------------|---------------------|-----------------------------------|------------------|------------------|------------------|
| Fort Sherman | wet | 566 \pm 13.9 | 555 \pm 107.67 | 10.93 (>10; <11) | 11 | 11.8 | 93.2 |
| Pipeline Road | middle | 552 \pm 15.3 | 918 \pm 194.44 | 14 | 14 | 14.8 | 94.6 |
| Playa Bonita | dry | 582 \pm 22.6 | 330 \pm 46.31 | 8.95 (>8; <9) | 9 | 9.1 | 98.9 |
| All sites | | 1700 | 1797 | | 14 | 14.2 | 98.6 |

Notes: S_{obs} represents the number of species observed, and S_{est} is the number of species estimated with the Michaelis-Menten Model (MMM) richness estimator. The 95% CI values in the rarefaction analyses were created based on the site with lowest abundance, Pipeline.

accounted for 23% of the total abundance index with $N = 393$, whereas seven species showed a total abundance index of <70 each (Appendix B). Survey completeness was above 90% at each site and for all sites together (Table 1), indicating sufficient sampling was performed to adequately depict ensemble structure.

Controlling factors and their spatial scale

Species richness (S), total abundance index (N), and total feeding attempts (F) mostly varied at the plot level rather than at larger scales (Table 2). At the site scale, only 20% of the variance was explained for S and <2% of the variance for N and F . The transect scale explained <7.2% of the variation for all emergent properties. The plot level explained the majority of the variation (63.6%) for S and >96% of the variation for N and F . Given that most of the variation was explained at the smallest scale, subsequent analyses were performed at this level.

Rainfall and temperature showed the highest correlation (0.77), so both variables were kept in the analysis. The first three principal components axes of total abundance index per species accounted for 77.9% of the variance, whereby the first component explained about half (49.6%) of the variance, the second 15.8%, and the third 12.4%. Habitat structure (HS), insects (IN), and climate (C) explained some, but not all of the variation in community properties, ranging from 82% of variance explained for the first principal component of community composition to just 14.5% explained for the total abundance index (N ; Table 3). On average, 42.8% of the variance was explained for all community properties. These explained variances substantially exceed the mean amount of variance explained in ecological literature (Møller and Jennions 2002). HS and a three-way undifferentiated explanation by climate/habitat structure/resources (HS+C+IN) explained most of the variation in the emergent properties. C, and in some cases C in addition to a multiway-undifferentiated group (HS+C+N or C+IN), explained most of the variance in three of the four species composition variables (SC, PCA1, PCA2). The fourth species composition variable (PCA3) was best explained by HS.

Patterns along the rainfall gradient

Among the univariate emergent properties, species richness (S) was significantly higher in the middle of the

gradient compared to the other sites. Furthermore, the wet and dry sites differed significantly from each other (Table 1). Total number of recorded feeding attempts (F) was higher in the middle of the gradient, followed by the wet and dry ends respectively; however, these differences were not significant (GLMM for F ; $df = 2$, $\chi^2 = 3.0$, $P = 0.22$; Table 2). Total abundance index (N) did not differ along the gradient (GLMM for N ; $df = 2$, $\chi^2 = 0.79$, $P = 0.67$; Table 2). Moreover, the distribution of the total abundance index (N) across transects within and among sites was also similar (Appendix C).

In contrast, species showed varying responses to the gradient. Some species had a higher total abundance index at the drier (e.g., *Myotis nigricans*) or at the wetter side of the gradient (e.g., *Pteronotus parnellii*). One was more abundant at the center of the isthmus (*Centronycteris centralis*), whereas other species were rare at all sites (e.g., *Cyttarops alecto*) (Fig. 2). *Centronycteris centralis*, *Cormura brevirostris*, *M. nigricans* and *Saccopteryx leptura* accounted for 64.7% of the total abundance index (N) and showed significant differences between sites (Appendix B).

DISCUSSION

Different community properties of the insectivorous bat ensemble along the rainfall gradient in Panama were influenced by factors that work at different spatial scales. According to our predictions, climate, operating at the largest scale, appeared to control species composition. Species richness and total abundance, however, were most influenced by habitat structure operating at a small scale. Species richness displayed a uni-modal response to the rainfall gradient, but contrary to our expectations, total abundance index (N) was not

TABLE 2. Variance partitioning for three community properties of aerial insectivorous bats across the Isthmus of Panama.

| Variable | Percentage of variance | | |
|----------|------------------------|----------------------------|-----------------------|
| | Species richness, S | Total abundance index, N | Feeding attempts, F |
| Site | 19.9 | 1.651×10^{-7} | 1.61 |
| Transect | 7.2 | 2.96 | 3.13×10^{-7} |
| Plot | 63.6 | 96.94 | 98.33 |
| Within | 9.3 | 9.55×10^{-2} | 6.21×10^{-2} |

TABLE 3. Variance partitioning for seven community properties of an insectivorous bat ensemble across the Isthmus of Panama.

| Properties | Percentage of variance | | | | | | |
|-------------|------------------------|----------|----------|-----------------------|-------|--------|--------|
| | Emergent properties | | | Community composition | | | |
| | <i>S</i> | <i>N</i> | <i>F</i> | SC | PCA1 | PCA2 | PCA3 |
| HS | 0.104 | 0.142 | 0.05 | 0.016 | 0.006 | -0.022 | 0.112 |
| IN | 0.041 | 0.022 | -0.001 | 0.017 | 0.001 | 0 | 0.02 |
| C | -0.001 | 0.066 | 0.009 | 0.184 | 0.226 | 0.45 | 0.008 |
| HS+IN | -0.003 | -0.003 | 0.022 | 0.006 | 0.006 | 0.003 | 0.000 |
| HS+C | 0.033 | -0.046 | 0.001 | 0.033 | 0.04 | 0.056 | -0.008 |
| C+IN | 0.035 | -0.045 | 0.004 | 0.137 | 0.23 | 0.148 | -0.023 |
| HS+C+IN | 0.106 | 0.010 | 0.009 | 0.144 | 0.308 | -0.021 | 0.028 |
| Unexplained | 0.684 | 0.855 | 0.95 | 0.463 | 0.182 | 0.386 | 0.864 |
| Total | 1 | 1 | 1 | 1 | 1 | 1 | 1 |

Notes: Abbreviations are: HS, habitat structure; IN, insect resources; C, climate; *S*, species richness; *N*, total abundance index; SC, species composition; and PCA1–3, principal component axes of species abundance index with highest loadings. SC is a multivariate response variable. In variance partitioning, negative values may occur (Oksanen et al. 2009).

affected by a change in climatic conditions. Overall, individual bat species showed distinct and statistically significant responses to the gradient, whereas emergent community properties responded mostly to small-scale differences in habitat structure.

Controlling factors across scales

Both climate and habitat structure have been hypothesized to exert a strong effect on bat assemblages (Walsh and Harris 1996, Lopez-Gonzalez 2004). On the one hand, physiological tolerances of Neotropical bats are expected to determine species distributions along temperature or moisture gradients (Ruggiero and Kitzberger 2004). Consequently, climatic variation should affect species composition. On the other hand, obstacle-rich areas (i.e., dense vegetation producing clutter) are expected to impose limits to flight maneuverability (Norberg and Rayner 1987) and, to a limited degree,

prey detection by echolocation (Schnitzler and Kalko 2001). Thus, an increase in vegetation density (or habitat structure) can reduce the number of species and the total number of bats capable of navigating and successfully foraging at small scales.

Our results support both hypotheses. We have shown that climate was the most important predictor of species composition (SC) and PCA1–2, suggesting that the niche might be largely determined by climate and not by small-scale variation in specific forest characteristics. If so, bats might be able to select where along the climatic gradient they achieve higher fitness, given their high mobility and low dispersal limitations (Wilson and Findley 1972, Stevens et al. 2007, Fahr and Kalko 2010, Jung and Kalko 2011). The results for the total abundance index (*N*) concur with other studies on insectivorous ensembles in temperate zones (Jaberg and Guisan 2001, Erickson and West 2003). However, other

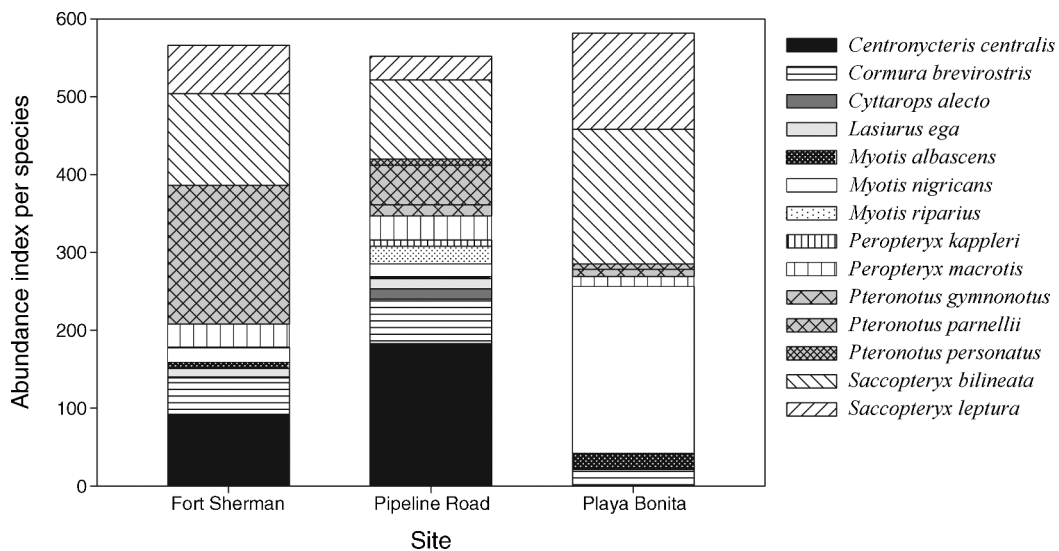


FIG. 2. Abundance index per species and total abundance index for three ensembles of aerial insectivorous bats across the Isthmus of Panama. Note the similarity of total abundance index across sites. Abundance index per species was calculated by pooling the occurrences across all visits per recording station per site.

studies have shown that climate has stronger effects on richness (S) at continental (Ruggiero and Kitzberger 2004) and regional scales (Lopez-Gonzalez 2004).

Simultaneously, we showed that habitat structure at the local scale was the most important predictor for S and N , highlighting the importance of microhabitat in determining the quantity of individuals present. Microhabitat characteristics (e.g., forest height, number of trees, gaps) are known to influence tropical and temperate bat, as well as bird, ensembles (MacArthur 1965, Schemske and Brokaw 1981, Ford et al. 2005, Estrada-Villegas et al. 2010, Fahr and Kalko 2010, Jung and Kalko 2011). These characteristics determine the density of obstacles, which is expected to limit flight maneuverability and, to a limited degree, prey location and discrimination via echolocation (Norberg and Rayner 1987, Schnitzler and Kalko 2001).

Finally, insect resources per se were not an important factor in structuring the ensembles, thus concurring with the prediction by Fenton (1990). However, we need to take into account several factors that might have compromised our results. Firstly, our insect sampling was unable to capture the full extent of the high spatial, temporal, and taxonomical variability of Neotropical insect assemblages (Smythe 1982). Secondly, sampling at the plot level, instead of the transect level, would have given a better assessment of food resources. Thirdly, similar studies on temperate systems have shown that both insect resources and habitat structure at the plot level affected bat community structure and species' abundances (Vindigni et al. 2009, Morris et al. 2010). Fourthly, even with a comprehensive and rather complete insect sampling, a tight link needs to be made between insect availability and actual use of by the various species of aerial insectivorous bats. Thus, our results give a first hint towards the role of insect abundance for bat ensembles, but the effect of insect resources on Neotropical insectivorous bats is an area of research that should be explored further.

How do we reconcile different mechanisms for different properties of community structure at different scales? We believe that at the larger scale, climatic variation might be the ultimate controlling factor through the mass effects paradigm (Shmida and Wilson 1985, Stevens et al. 2007) to explain the variation in community composition. The ensemble we studied might have the dispersal potential to be anywhere across the isthmus. If so, mass effects at the species level can determine their abundances because individuals are capable of moving from source to sink patches and track suitable resources and conditions across the landscape. Once in suitable patches, habitat structure can be a proximal controlling factor at small scales because it regulates total abundance index and might restrict which species can coexist at this scale. These two simultaneous mechanisms might be more prevalent than previously reported; for example, Fahr and Kalko (2010) have also suggested that climate, which promotes

habitat heterogeneity at large scales, helps to determine community composition and turnover, whereas vegetation complexity (i.e., habitat structure) at small scales influences species richness. We are aware that other factors that have not been included in the analysis, such as topography or habitat modification, might influence community structure directly or indirectly. However, there are no cave systems along the isthmus that would influence species occurrences or abundances and sites were selected due to their high forest cover, thus, we presume that the effect of topography and habitat modifications might be rather low.

Community properties along the rainfall gradient

Total abundance index (N) across the climatic gradient was strikingly constant despite significant differences in species richness (S). It is expected that more rainfall leads to higher plant productivity, and this should cascade to richer and more abundant animal ensembles (Rosenzweig 1995). Interestingly, our results suggest a different relationship. Variation in S with minimal variation in N suggests density compensation according to the definition of Gonzalez and Loreau (2009). The three assumptions for compensation were met in our system. First, we can assume that the ensemble we studied is likely to be resource limited, for instance, with regard to roosting sites (e.g., caves or large trees with buttresses [Kalko 1998, Hoffmann et al. 2007]), although we did not assess roosting availability. Second, we have no evidence to assume that our system is isolated from the regional pool of species, and it represents an open community given that there are no isolating barriers such as mountain ranges. Third, resources should be constant across sites (Ernest and Brown 2001), and our results indicate that insect abundance and biomass were not statistically different across the isthmus (insect abundance ANOVA, $F_{2,42} = 0.84$, $P = 0.44$; biomass ANOVA, $F_{2,42} = 2.15$, $P = 0.13$). We can envisage two mechanisms by which compensation might occur. First, species that are able to tolerate drier conditions might reach higher abundances because of competitive release; so summing their abundances might add up to the total abundance index (N) of the other sites. Second, larger species might exclude smaller species where rainfall is higher because the former are usually more abundant in those areas and tend to take a greater share of resources (Cohen et al. 2003). Hence, lower total abundance index (N) at the wettest site. In our system, it is plausible that *Pteronotus parnellii*, the largest species in the ensemble (22.5 g, average mass in the Barro Colorado Nature Monument; C. Meyer, *personal communication*), might outcompete smaller species (e.g., *Myotis nigricans*), not only due to the size advantage, but because *P. parnellii* has higher flight speeds than other species in the ensemble (Norberg and Rayner 1987), and faster travelers tend to monopolize resources because they are able to find them first (Brown 1989). Nonetheless, displacement by competition merits

further research because *P. parnellii* uses a different echolocation system than the other aerial insectivorous species and is able to forage within dense vegetation (Schnitzler and Kalko 2001). Hence, the observed differences in abundance might stem from other mechanisms that we did not include in our analysis.

Species richness showed a uni-modal distribution, in agreement with Mittelbach et al. (2001), Whittaker (2010), and our predictions. This raises the question: Which factors might explain why richness decreases at the wetter and more productive sites? One explanation invokes a change in competitive structure (see previous paragraph). Another explanation relies on the “environmental heterogeneity” hypothesis (Rosenzweig 1995), which predicts that increased productivity reduces habitat heterogeneity, and consequently, richness. In support of this, the rainiest site in the isthmus, compared to the site with intermediate rainfall, had fewer treefall gaps and streams as well as lower canopies, but greater number of trees (number of trees ANOVA, $F_{2,102} = 6.08$, $P = 0.003$; Tukey’s HSD between wet and dry, $P = 0.003$; wet and middle, $P = 0.029$; middle and dry, $P = 0.74$). This trend in forest structure is also supported by data from various larger forest plots across the isthmus (Condit 1998). A reduction in “environmental heterogeneity” with an increase in the number of obstacles may reduce richness because niche diversity drops and flight maneuverability of bat species becomes a critical issue determining which species can fly and forage efficiently at a site. This might be an explanation for the decline of species richness at the driest site as well. Dry sites had the highest vertical forest density and the shortest canopies across the isthmus (foliage structure ANOVA, $F_{2,102} = 8.01$, $P < 0.001$; Tukey’s HSD between wet and dry, $P < 0.001$; wet and middle, $P = 0.83$; middle and dry, $P = 0.006$; canopy height ANOVA, $F_{2,102} = 27.46$, $P < 0.001$; Tukey’s HSD between wet and dry, $P < 0.001$; wet and middle, $P = 0.56$; middle and dry, $P < 0.01$). However, the decrease in richness with increasing dryness in the isthmus could also be linked to a reduction of roosting sites or habitat availability through anthropogenic alterations accumulated over time (Condit et al. 2001). Hence, we cannot rule out that anthropogenic perturbations at the dry end of the gradient produce a species-poor insectivorous bats ensemble as reported by Jung and Kalko (2010, 2011). In sum, although a uni-modal distribution between species richness and rainfall or productivity is expected to be more common than other distributions, the underlying mechanisms responsible for this pattern remain to be explored further.

CONCLUSIONS

We were able to show that individual Neotropical insectivorous bat species and different levels of community composition showed a strong response to climate at the largest scale of analysis. In contrast, habitat structure variables were the most important determi-

nants of emergent community properties at small scales, implying that tolerances to high habitat structure or heterogeneity within the habitat influence patch use and species coexistence. Our results highlight the importance to incorporate simultaneously spatial scale and different controlling factors to explain different and complementary measures of community structure. It is known that biodiversity studies must begin to recognize that the factors that structure communities are strongly scale dependent (McGill 2010) and that several properties of the community need to be assessed in this fashion. Ultimately, the study of natural and anthropogenically modified communities need to assess simultaneously (1) several controlling factors in an explicit environmental gradient, (2) how these factors vary with scale, and (3) how this scale dependency affects different community properties. We believe that this approach will lead to a far better understating on how and why communities are structured the way they are.

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SUPPLEMENTAL MATERIAL

Appendix A

Detailed methods for sound recordings, sound analysis, and parameters for identification of difficult species (*Ecological Archives* E093-101-A1).

Appendix B

Abundance index and feeding attempts per species and for all sites across the Isthmus of Panama compared with LMMs and Tukey multiple comparisons test (*Ecological Archives* E093-101-A2).

Appendix C

Total abundance index per transect at three sites across the Isthmus of Panama (*Ecological Archives* E093-101-A3).