1 Correlates of Cave-Roosting Bat Diversity as an Effective Tool to Identify Priority Caves

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Abstract – Cave ecosystems are subterranean biodiversity hotspots, but limited knowledge of the distribution of diversity among caves hampers their conservation. Surveys of surrogate taxa (e.g., keystone species) can identify hotspots of biodiversity when knowledge about an ecosystem is lacking. Bats are keystone species in cave ecosystems because their guano is the primary energy source supporting diverse assemblages of cave-dependent wildlife. However, directly measuring bat diversity is time-consuming and requires expert knowledge; instead, we suggest the use of correlates of bat diversity that can be derived from readily accessible data (e.g., land-use maps) and straightforward methods not requiring expert knowledge (e.g., cave surveys, interviews) as a foundation for prioritizing caves. To identify easily measurable correlates of bat diversity, we compared assemblage composition and species abundances of 21 bat species captured in 56 caves on Bohol Island, Philippines, along gradients in environmental factors and human disturbance. Model- and distance-based methods indicated that surface-level disturbance (i.e., percent non-forested habitat, degree of urbanization and road development) along with cave complexity (i.e., available roosting area, structural heterogeneity, number of entrances and temperature range) were the most influential factors governing cave-roosting bat assemblages, thus representing correlates of bat diversity. Prioritization schemes based on these correlates select combinations of caves with greater species richness than both random selection and selection of caves based on observed richness from intensive bat surveys. The use of easy-to-measure environmental and disturbance correlates of bat diversity is an effective tool to prioritize caves to protect cave-roosting bats and the cave-dependent wildlife they support.

1. Introduction

Setting conservation priorities for the allocation of limited financial resources is a difficult task faced by conservation organizations, including government agencies responsible for the protection and management of native biodiversity. Perhaps the most widely-adopted approach to priority-setting is to identify hotspots of biodiversity based on the number of endemic species and degree of human threat (Myers et al., 2000). Many subterranean ecosystems, such as caves, warrant designation as biodiversity hotspots given the high proportion of endemic species (Whitten, 2009), especially invertebrate taxa (Deharveng and Bedos, 2012), they support. Many cave endemic species are relatively small, often poorly studied and are rarely considered in conservation priority setting, yet their habitats are under intense human pressure (Deharveng and Bedos, 2012; Whitten, 2009). Mining for nonrenewable sediment deposits (e.g., limestone and phosphate) is the most severe threat to cave ecosystems (Culver and Pipan, 2009; Furey and Racey, 2016), at times resulting in the complete destruction of caves (Calò and Parise, 2006). Dumping of household waste and agricultural practices that increase sedimentation and pesticide contamination pollute cave ecosystems (Culver and Pipan, 2009; van Beynen et al., 2012, Watson et al., 1997). In the absence of designated walkways, foot traffic from tourists can compact cave substrates and trample floor-dwelling cave wildlife (Watson et al., 1997). Moreover, tourists unintentionally alter microclimatic conditions, leading to marked fluctuations in carbon dioxide levels, air temperature and relative humidity (Furey and Racey, 2016), making caves uninhabitable for some cave-dependent species (Russell and MacLean, 2008). Unfortunately, cave ecosystems are often simultaneously subjected to multiple threats (Culver and Pipan, 2009; Furey and Racey, 2016).

To formulate effective conservation strategies to protect cave ecosystems, it is fundamental to characterize the biodiversity dependent upon caves, but taxonomic information

about many cave taxa (e.g., invertebrates) is lacking (Elliott, 2005). In such instances, surrogate taxa (e.g., keystone, umbrella and indicator species) (Caro, 2010) can be used to identify hotspots of biodiversity (Martikainen et al., 1998; Suter et al., 2002). Although the use of surrogate taxa to prioritize ecosystems is debated (Andelman and Fagan, 2000; Sætersdal and Gjerde, 2011), species that play keystone roles in structuring trophic networks within ecosystems should serve as centerpieces for prioritization decisions (Mills et al., 1993; Power et al., 1996). Because cave ecosystems lack primary producers, cave-roosting bats are keystone species in cave ecosystems as they support diverse assemblages of cave-dependent wildlife via the deposition of guano (Gnaspini and Trajano, 2000; Kunz et al., 2011). Guano is the primary energy source sustaining bottom-up dynamics in caves by supporting coprophagous invertebrates, which in turn are prey for larger vertebrate predators (e.g., cavefishes, salamanders) (Gnaspini and Trajano, 2000). For example, grotto salamanders (*Eurycea spelaea*), top cave predators, depend on invertebrates that congregate on guano piles formed by roosting gray bats (*Myotis grisescens*) to such an extent that body condition varies with the presence of this migratory bat species (Fenolio et al., 2014). Bat species differ in their diets (e.g., insects, nectar, fruit), and as a result, their guano varies in physiochemical and nutritional properties (e.g., pH, organic matter, minerals) (Emerson and Roark, 2007; Studier et al., 1994). Conserving diverse aggregations of cave-roosting bats therefore supports a diversity of coprophagous invertebrates and their predators (Ferreira et al., 2007; Trajano and Bichuette, 2010). Some of the largest and most diverse aggregations of bat species in the world roost in caves (Hutson et al., 2001), with roughly 40% of all threatened bat species using caves as roosts (IUCN, 2015). Yet cave bat populations continue to decline globally, with cave disturbance identified as the leading

cause of these declines (Hutson et al., 2001). Ultimately, the loss of cave-roosting bats will have cascading effects on cave ecosystems.

Prioritizing caves based on in-depth knowledge of the compositions of cave bat assemblages would effectively conserve imperiled bat species and diverse cave ecosystems. However, identifying caves that house large, diverse aggregations of bats requires expert knowledge of bat species and can be time-consuming and expensive. Instead, we suggest use of correlates that reflect increased bat diversity and abundance that are readily accessible, easy-to-use and require minimal training to measure accurately. In the present study, we identify correlates of cave-roosting bat diversity using easily acquired data and straightforward methods. We then test their efficacy as a tool for identifying priority caves to promote bat conservation. First, we compared species composition and abundance of cave bat assemblages on Bohol Island, Philippines, with a suite of environmental and human disturbance factors that can be measured in just a few hours to identify which factors correlated with increased bat diversity. Then, we developed cave prioritization schemes based on the identified correlates of bat diversity and tested the performance of each scheme for selecting caves that conserve the greatest species richness in comparison to random selection and selection of caves based on our knowledge of observed richness. All prioritization schemes outperformed random selection, and the scheme that combined measures of surface-level disturbance and cave complexity conserved the most species. Surface-level disturbances can be measured using open-source data and cave complexity using rapid caves surveys and interviews with local residents. We demonstrate that basic resources available to government agencies, and other conservation organizations charged with protecting biodiversity, can be used as an effective prioritization tool to protect diverse bat assemblages and the cave-dependent wildlife they support.

2. Methods

2.1. Study sites

Bohol Island is located in the central Visayas region of the Philippines and covers an area of approximately 4,100 km² that is largely composed of limestone karst (Urich et al., 2001). Preliminary reconnaissance work and informal conversations with local residents, cavers and other researchers identified numerous caves on Bohol Island. We selected 62 caves subject to a gradient of human disturbance, including undisturbed caves within protected areas, disturbance from local residents who extract cave resources and more severe disturbance from active tourism and mining operations (Fig. 1). Final selection of caves was made based on knowledge of the presence of cave-roosting bats. Caves were visited between July 2011 and June 2013, with the exception of January – May 2012.

2.2. Bat surveys

Bats were captured using mist nets placed in strategic locations at cave entrances and inside passages for two consecutive nights at each cave, with all other potential exits blocked with vegetation. Various-sized nets (i.e., 3, 6, 9 and 12 m) were erected in the same location for both nights and opened just prior to sunset then continuously monitored, on average, for 5.5 hours per night. Captured individuals were identified to species using morphological characteristics (Ingle and Heaney, 1992), then weighed (g) and forearm measured (mm). Prior to release, a 3 mm wing biopsy punch of the right plagiopatagium was taken to mark individuals to avoid including recaptures in analyses (Faure et al., 2009). Because all cave exits were blocked by mist nets and/or vegetation, sampling effort was calculated as the number of hours the net(s)

was open (nh) for both nights. Sampling effort was not calculated as net-meter-hours (nmh) because caves supporting comparable populations of bats could vary in size and number of entrances and, consequently, would skew, either inflate or dilute, the capture rate if expressed in net-meter-hours. Raw count data were corrected for differing sampling efforts among caves, yielding adjusted capture rates (individuals/nh) for each species at each cave.

For each species, except *Cynopterus brachyotis* and *Eonycteris spelaea*, at least one adult individual was prepared as a voucher specimen and deposited in the Natural Science Research Laboratory of the Museum of Texas Tech University. All methods followed guidelines set forth by the American Society of Mammalogists (Sikes, et al., 2011) and were approved by the Texas Tech University Animal Care and Use Committee (ACUC 10015-04, 13031-04).

2.3. Quantifying explanatory factors

2.3.1. Environmental factors

Each cave was mapped using standard cave survey methods (Ellis, 1976), with most surveys taking less than two hours. A series of survey stations, the first station being located at the main entrance, was established along the length of the cave based on changes in height or width of the cave passage or presence of side passages. We made great efforts to survey all passages in each cave, with only four instances in which a passage was not surveyed due to safety concerns. At each station, distance to the previous station and height and width of the cave passage were measured using a tape measure. If passage height was unreachable, a laser rangefinder was used or height was visually estimated. Number of cave entrances, including vertical entrances, was also recorded. Additionally, ambient temperature (C°), wind speed (kmh)

and relative humidity (%) were measured at each station using a hand-held weather station (Kestrel 3000 Pocket Weather Meter).

We estimated available roosting area and structural heterogeneity of each cave using measurements from cave surveys. Following methods detailed by Brunet and Medellín (2001), total surface area of a cave was based on a series of elliptical cylinders represented by length, height and width measurements taken between survey stations. Surface area was calculated using the formula $C = 2\pi L([a^2 + b^2]/2)^{1/2}$, where L is the length between survey stations and a and b represent height and width of the passage between survey stations, respectively. Surface area was summed across survey stations and halved to approximate the roosting area available to bats in each cave. Structural heterogeneity refers to the complexity of chambers and passages within a cave and was calculated by dividing the total cave length by the greatest length between any two survey stations (Arita, 1996). With increasing structural heterogeneity, a cave is assumed to have a greater diversity of available roosting sites. Single tunnel caves have a structural heterogeneity of 1.0, with an increasing value indicating increasing structural heterogeneity.

Variation in microclimatic conditions (i.e., temperature, humidity) has been shown to influence roost selection by cave-roosting bats (Avila-Flores and Medellín, 2004; Brunet and Medellín, 2001). Therefore, we included measures of variation in microclimate using measurements of ambient temperature and relative humidity taken during cave surveys. Specifically, we calculated the range in values by subtracting the minimum value from the maximum value. Wind speed was not included in our analysis since most caves had no measurable wind movement or lacked any variation in wind speed.

2.3.2. Human disturbance factors

We modified the karst disturbance index developed by van Beynen and Townsend (2005) to include a framework of potential cave disturbances that may impact cave-roosting bat assemblages and incorporated additional human disturbance factors by interviewing local residents. Human disturbance was assessed at the surface- and subsurface-level, with multiple indicators of disturbance at each level (Table 1). We assigned each indicator a score ranging from 0 to 3 depending on the extent and severity of the human disturbance: 0 – none, 1 – localized and not severe, 2 – highly disturbed and widespread, 3 – severely disturbed (van Beynen and Townsend, 2005).

Surface-level disturbances - Cave locations were georeferenced using a global positioning system unit and plotted using Google Earth Pro, a freely available online resource for satellite imagery, to gauge surface-level disturbance within a 1 km radius of the main cave entrance. We included visual observations of surface-level disturbances as a supplement when satellite images from Google Earth Pro (2011 – 2015) were obscured by dense cloud cover. We selected a 1 km radius since many bat species remain near the roost if quality foraging habitat (i.e., intact forest) is present locally (Kingston, 2013); thus, disturbances at this scale could make a cave unsuitable due to the increase in energetic costs of commuting greater distances to available foraging habitat. Within 1 km radius of each cave, we estimated the percentage of non-forested habitat (%), number of human residents (i.e., number of habitations * average household size of 4.79 individuals on Bohol Island; Philippine Statistics Authority, 2013) and road size as indicators of human development surrounding the cave (Table 1).

Subsurface-level disturbances – Information regarding human disturbance at the subsurface level was obtained through visual observations during cave surveys and one-on-one interviews with local residents. Percentage of the cave area impacted by mining, typically from

the extraction of limestone and/or phosphate, was estimated visually during cave surveys, along with household waste and vandalism/graffiti. Furthermore, modifications of the cave structure to accommodate humans (e.g., tourists, miners) were observed and scored based on increasing invasiveness.

One-on-one interviews using a structured questionnaire composed of closed-format questions were conducted to collect data on subsurface-level disturbances by residents living in close proximity to caves (1 – 2 km). We interviewed, on average, 10 individuals from different households living near each cave, which took typically less than an hour but duration varied depending on the number of interviewers. Local residents (n = 559) were asked about the frequency and purpose of visits (e.g., tourism, guano or swiftlet nest collection, bat hunting and/or religious purposes) to the cave, both by themselves and others in the *barangay* (village or subunit of a city). Interviewee responses to these questions allowed us to score resource extraction, bat hunting and visitation frequency. Specifically, we summed the number of responses indicating that the resident or someone they knew visited the cave to extract resources or hunt bats and divided by the total number of responses. Scores for both factors were confirmed with visual observations of human activities indicative of resource extraction (e.g., sacked guano, shovels and buckets) and bat hunting (e.g., nets strung between poles to catch bats, burned palm fronds and/or rubber to suffocate roosting bats) during cave surveys. Visitation frequency was based on greatest visitation frequency (i.e., daily, weekly, monthly or yearly/never) indicated by two or more interviewees.

Additional factors – In addition to georeferencing cave localities, the center of the nearest *barangay* was georeferenced and plotted online using Google Earth Pro. The Euclidean distance between the cave and *barangay* center was measured (km), as well as the distance from

the cave to nearest access point (km) (e.g., foot trail, road). Geospatial data delineating protected areas, including watershed forest reserves, protected landscapes and seascapes and national monuments, identified under the National Integrated Protected Areas System were obtained via the freely accessible website maintained by the Department of Environment and Natural Resources of the Philippines (<http://www.bmb.gov.ph/>) and plotted with cave localities in Google Earth Pro. Caves that were located within the boundaries of a protected area were scored binarily: 1 (cave within boundaries of protected area) or 0 (outside boundaries).

2.4. Statistical analyses

Prior to statistical analyses, thorough data exploration was carried out to check for outliers, heterogeneity of variance, deviations from normality and other potential issues pointed out by Ieno and Zuur (2015). Continuous data were tested for normality using the Shapiro-Wilk test, with non-normally distributed data $\log_{10}$ -transformed to improve normality. Of the 62 caves included in this study, six were removed from analyses due to missing data (e.g., microclimate values were not measured due to equipment malfunction). All analyses were conducted in R version 3.1.2 (R Core Team, 2014).

Principal component analysis (PCA) was used to reduce the dimensionality of the dataset. All environmental and human disturbance factors (transformed if improved normality) were used as inputs to function *princomp* in base package *stats* (R Core Team, 2014). The PCA, based on a correlation matrix, extracted six components with eigenvalues greater than 1.0 (Kaiser, 1960). Combined, the first six components explained 73.9% of the variance in caves (Table 2). All meaningful loadings (i.e., loadings > 0.30) (Harlow, 2014) were included in the interpretation of principal components (PC).

The first component (PC1) was positively associated with surface-level disturbances (i.e., percent non-forested habitat, degree of urbanization and road development) and negatively associated with distance to access. All environmental factors, with the exception of humidity, loaded positively on the second component (PC2). Caves with increasingly positive scores on PC2 are characterized by increasing complexity, those having greater available roosting area, structural heterogeneity, number of entrances and range in temperature. The third component (PC3) was positively associated with mining and household waste but negatively associated with a wide range of microclimatic conditions. Thus, high scores on PC3 describe caves with stable microclimates that experience human disturbances that include mining and/or dumping of household waste. The fourth component (PC4) was positively associated with cave development and visitation frequency but negatively associated with resource extraction. Caves with high scores on PC4 were frequently visited and had greater development of the cave (e.g., installed lighting, walkways) but were not exploited for swiftlet nests, speleothems or any other resource. Resource extraction, range in humidity, protected area and visitation frequency was positively associated with the fifth component (PC5), representing caves likely found within protected areas that are subjected to resource extraction and frequent visitation with stable humidity levels. The sixth component (PC6) was positively associated with bat hunting, household waste and protected area but negatively associated with mining. Caves with high scores on PC6 were likely located within the boundaries of a protected area but experienced bat hunting as the primary form of human disturbance.

To examine variation in species composition among assemblages ($n = 56$), we used a multivariate generalized linear model with principal components (PC1 – PC6) as predictor variables using the *manyglm* function in the package *mvabund* (Wang et al., 2014). Negative

binomial regression structure was specified in our models due to overdispersion of the species composition data. The *anova.manyglm* function in *mvabund* was used to test for significant effects of predictor variables on assemblage composition, with post-hoc univariate tests used to determine the responses of individual species. We report responses of species with unadjusted *p*-values. Diagnostic plots were checked to ensure that model assumptions were met.

To visualize the variation in bat assemblage composition in relation to our predictor variables, we conducted indirect gradient analysis using non-metric multidimensional scaling (NMDS) on the site-species matrix. Ordinations based on Manhattan dissimilarity coefficients were conducted using function *metaMDS* in package *vegan* (Oksanen et al., 2015). We superimposed computed vectors for predictor variables onto the ordination plot using function *envfit* in *vegan* to determine which variables have the greatest influence on assemblage structure. The significance of the fitted vectors was assessed after 999 permutations, with resulting correlation values (r^2) indicating the strength of the association between each predictor variable and the configuration of assemblage composition in the NMDS ordination.

Identification of significant correlates of composition structure and species abundance of cave-roosting bats allowed us to prioritize caves for bat conservation. To test the performance of our proposed prioritization schemes based on identified correlates in comparison to random selection, we compared the number of species conserved when selecting roughly 10% of caves (i.e., 6 caves) in our study. Based on principal component scores, we selected six caves based on three prioritization schemes: Scheme 1 - caves with the highest negative scores on PC1 (surface-level disturbance); Scheme 2 - caves with the highest positive scores on PC2 (cave complexity); and Scheme 3 - a combination of Schemes 1 and 2 (caves with a combination of both negative scores on PC1 and positive scores on PC2). Next, we randomly selected six caves without

replacement from a pool of all 56 caves, summing species richness during each of the 999 repetitions. We adjusted species richness for varying sampling effort at each cave and compared with unadjusted species richness, the results did not differ so we elected to report unadjusted species richness. Observed cumulative species richness from six caves selected based on our prioritization schemes were then compared with the distribution of cumulative species richness of random selection. In addition, we also compared the observed cumulative species richness of our prioritized caves with that of the six most species-rich caves in our study.

3. Results

We surveyed 62 caves across Bohol Island from July 2011 - June 2013 to collect data on environmental and human disturbance factors simultaneously with bat composition (Appendix A). After 655 net-hours, we captured 7,522 bats of 23 species (Appendix B). These captures represent 69.6% of the 33 bat species reported on Bohol Island (Sedlock et al., 2014), in addition to the first published records of *Chaerephon plicatus* and *Taphozous melanopogon* on Bohol Island, though *T. melanopogon* was acoustically recorded previously by Sedlock et al. (2014). Of the species on Bohol Island that were not captured during our study, all are forest-roosting species (e.g., *Kerivoula*, *Murina*, *Pteropus*, *Acerodon*) except *Hipposideros bicolor*, which remains taxonomically unresolved and of uncertain distribution in the Philippines.

Because of missing environmental factor values from six caves, we included a subset of 56 caves in our analyses (Appendix A). From this subset of caves, we captured 6,823 bats, excluding recaptures, of 21 species, representing the families Emballonuridae, Hipposideridae, Megadermatidae, Molossidae, Pteropodidae, Rhinolophidae and Vespertilionidae. *Hipposideros*

diadema was the most abundant species, representing 31% of all captures, followed by *Miniopterus schreibersii* (14.8%) and *M. australis* (14.2%).

Model-based analysis using *mvabund* revealed surface-level disturbance (PC1, $p = 0.003$) and cave complexity (PC2, $p = 0.020$) as significant variables shaping the assemblage composition of cave-roosting bats on Bohol Island (Table 3). Abundance for a majority of species (61.9%) declined with increasing surface-level disturbance, with two species significantly influenced. *Emballonura alecto* and *Hipposideros pygmaeus* responded negatively to surface-level disturbances, with decreasing abundance in caves with a lower percentage of intact forest cover and located near major roadways and urban areas. Conversely, *Myotis macrotarsus* and *Rousettus amplexicaudatus* responded positively to surface-level disturbance. Over three-quarters (76.2%) of bat species exhibited increases in abundance with increasing cave complexity, with six species significantly influenced. Several *Rhinolophus* species, along with *Hipposideros diadema* and *Miniopterus tristis*, responded positively to increasing cave complexity. Abundance of these species increased in caves with greater roosting area, structural heterogeneity, number of entrances and range in temperature. Only one species, *Hipposideros obscurus*, responded negatively to increasing cave complexity.

No other factors exhibited a significant influence on assemblage composition in the *mvabund* analysis ($p > 0.14$). Mining (PC3) explained the least amount of deviance in assemblage composition (Dev = 23.07, $p = 0.539$) and had no significant influence on any individual species' abundance, with the exception of *Hipposideros ater* which exhibited a marginal response ($p = 0.04$) (Table 3). However, several species exhibited a significant response in abundance to at least one of the remaining three principal components (PC4 – 6, Table 3). *Taphozous melanopogon* had higher abundance in caves with high levels of cave development

(PC4); those in which lighting systems, paved walkways and/or other modifications to the cave environment had been made to accommodate human activities (e.g., mining, tourism). Conversely, *Hipposideros diadema* was lower in abundance in such caves. Two species, *Cynopterus brachyotis* and *Myotis macrotarsus*, responded negatively to increasing resource extraction and human visitation frequency in caves within the boundaries of protected areas. *Miniopterus australis* responded negatively to bat hunting (PC6), yet *Rousettus amplexicaudatus* had highest abundances in caves with greatest hunting pressure. This is likely the result of *R. amplexicaudatus* being a species targeted for human consumption.

Non-metric multidimensional scaling (NMDS) allowed us to visualize sites (caves) and species in two-dimensional space (Fig. 2; stress = 0.15), though caves were removed from the final NMDS biplot to reduce clutter. Plotting vectors using *envfit* (distance-based method) gave similar results to *mvabund* (model-based method), and corroborated that surface-level disturbance (PC1) and cave complexity (PC2) were the most influential variables governing assemblage composition ($r^2 = 0.101$, $p = 0.048$; $r^2 = 0.180$, $p = 0.007$, respectively). Species situated in the upper left of the NMDS plot (Fig. 2) tend to occupy complex caves that experience greater surface-level disturbances. Bat hunting (PC6) exhibited a marginal influence on assemblage composition ($r^2 = 0.105$, $p = 0.053$), with *R. amplexicaudatus* abundance correlated with increasing hunting pressure.

Both model-based and distance-based methods pointed to surface-level disturbances (PC1) and cave complexity (PC2) as the most influential variables shaping bat assemblages in caves on Bohol Island. Selection of six caves based solely on low levels of surface-level disturbance (Scheme 1) resulted in the protection of 13 species (61.9% of all captured species, Fig. 3), high cave complexity (Scheme 2) also protected 13 species (61.9%) and the combination

of both variables (Scheme 3) protected 15 species (71.4%). Random selection of six caves resulted in the protection of 12 species, on average, with a range between 9 – 15 species (95% confidence intervals, Fig. 3). All prioritization schemes protected more species than those protected, on average, when caves were selected randomly (12 vs. 13 - 15 species); thereby indicating that prioritization based on any one of our proposed schemes will outperform random selection of caves. However, when compared to the cumulative species richness from six caves with the greatest number of captured species in our study (14 species), only Scheme 3 protected more species (15 species; Fig. 3).

4. Discussion

We demonstrate, for the first time, that cave-roosting bat assemblages are significantly influenced by both environmental factors and human disturbance of caves. Assemblage diversity responded negatively to increasing levels of surface-level disturbance, specifically decreased forest cover with increased urbanization and road development, but responded positively to increasing cave complexity, including all measured environmental factors with the exception of humidity. Similar patterns were also detected in abundances for a majority of the 21 species in our study. Thus, we considered surface-level disturbance and cave complexity to represent correlates of cave bat diversity. Using these identified correlates to prioritize 10% of the 56 caves in our study ($n = 6$) resulted in the protection of more cave-roosting bat species than random selection of caves as well as more species than the cumulative species richness of the top six species-rich caves in our study. This demonstrates that correlates of bat diversity can be a useful tool for prioritizing caves to promote the conservation of cave-roosting bats. As keystone species in cave ecosystems, the protection of diverse assemblages of bats will provide an umbrella of

protection for other cave-dwelling wildlife, particularly coprophagous invertebrates dependent upon bat guano as a primary energy source (Gnaschini and Trajano, 2000; Kunz et al., 2011).

Interestingly, changes in assemblage composition and species abundances of cave-roosting bats varied depending on the scale: surface-level (landscape surrounding the cave in a 1 km radius) or subsurface-level (subterranean). At the surface level, decreasing forest cover, combined with increasing urbanization and development of roadways, contributed to significant differences in assemblage composition of cave-roosting species in our study. Not surprisingly, 13 species (62%) also responded negatively to increasing surface-level disturbances surrounding the cave, likely because such surface-level disturbances were correlated with increased accessibility to the cave (i.e., decreased distance to roads, trails and foot paths). Cave-roosting bats exhibit high roost fidelity (Lewis, 1995), so any reduction in forest cover surrounding a cave may result in increased commuting costs to reach suitable foraging grounds or risk foraging in suboptimal grounds (Kingston, 2013). Forest loss and increasing pressures from urbanization and development pose serious threats to bat populations worldwide (Jung and Threlfall, 2016; Meyer et al., 2016), such disturbances should be used as a gauge for prioritizing caves to improve bat conservation.

At the subsurface-level, human disturbance, of any form, did not significantly shape assemblage composition. Most interestingly, mining did not influence compositional structure and only significantly affected the abundance of one species in our study. Mining operations on Bohol Island tend to be on a smaller scale than is typical in Southeast Asia (Clements et al., 2006), with most extraction conducted manually by workers rather than by machinery, which may have contributed to our results. Other forms of human disturbance had mixed effects on the abundances of individual species. For example, cave development had a positive effect on the

abundance of *Taphozous melanopogon*; however, *Hipposideros diadema* were significantly less abundant in these caves. Bat hunting had differing effects on the abundance of *Rousettus amplexicaudatus* and *Miniopterus schreibersii*. Hunting pressure was highest in caves with large aggregations of *R. amplexicaudatus*, a species targeted for human consumption throughout its range in Southeast Asia (Csorba et al., 2008). Though assemblage composition was not influenced by human disturbance at the subsurface-level, population abundances of most species declined in caves with increasing levels of subsurface-level disturbances.

Conversely, at the subsurface-level, all of the measured environmental factors, with the exception of humidity, exerted a significant influence on the composition of bat assemblages. Numerous studies have shown a positive correlation between assemblage attributes (e.g., species richness and diversity, overall abundance) and available roosting area (Brunet and Medellín, 2001; Luo et al., 2013), total cave length (Arita, 1996; Cardiff, 2006), entrance dimensions (Cardiff, 2006) and degree of chamber and passage complexity (Arita, 1996; Brunet and Medellín, 2001; Cardiff, 2006). Microclimatic conditions have also been shown to influence roost selection by cave bats, particularly temperature (Avila-Flores and Medellín, 2004; Furey and Racey, 2016). Our study shows that environmental factors collectively promote a richer assemblage composition and increase abundances of a majority of species. Results from our study combined with the findings of other studies demonstrate clearly that the protection of large, complex caves will conserve a greater diversity of cave-roosting bats.

Caves are critical roosting sites for many bat species, including many threatened species, and need to be protected to maintain high bat diversity. For instance, caves and other subterranean habitats (e.g., abandoned mines, military fortifications) support 77% of the bat fauna in China, including 30 species classified as nationally endangered or vulnerable (Luo et al.,

2013). Similarly, 80% of the bat species in Puerto Rico roost in caves (Rodríguez-Durán, 2009). Our results demonstrate that species composition and abundance of cave-roosting bat assemblages are shaped by both human disturbance at the surface-level and environmental factors at the subsurface-level and are therefore correlates of bat diversity. When we prioritized caves based on these easily measurable correlates, all of our prioritization schemes (1-3) lead to the protection of more species of cave-roosting bats than were protected, on average, when randomly selecting caves, indicating that correlates of bat diversity identified by this study are effective at prioritizing caves. However, only Scheme 3, which prioritized caves based on both surface-level disturbance and cave complexity, resulted in the cumulative protection of more species than were observed across our six most species-rich caves. Based on our findings, to safeguard diverse assemblages of cave-roosting bats and the ecosystems they support, we advocate for the protection of caves with combined high cave complexity and minimal surface-level human disturbance.

Both our model- and distance-based methods pointed to cave complexity as having the strongest effect on assemblage composition and species abundances, followed by surface-level human disturbance. Therefore, we suggest that identification of candidate caves for protection follow a systematic process. Prioritization efforts should first focus on cave complexity, which can be assessed using standard cave surveys that can be completed in less than two hours and require minimal training. Prior to conducting cave surveys, it is wise to contact local officials to confirm the presence of cave-roosting bats to avoid wasting time and financial resources. In some countries, cave maps, from which cave complexity can be measured, have already been created by speleological clubs (e.g., Shepton Mallet Caving Club, Texas Speleological Society) and government agencies (e.g., Department of Environment and Natural Resources of the

Philippines), and these often include information about the presence of cave-roosting bats. Prioritization should then be refined by gauging levels of human disturbance in the landscape surrounding the cave, selecting those caves with minimal landscape disturbance. This can be evaluated from open-access sources, such as Google Earth and nonprofit- or government-managed land cover repositories (e.g., U.S. Geological Society Landsat Mission, National Mapping and Resource Information Authority of the Philippines). Finally, while our systemic process allows for a subset of candidate caves to be identified out of potentially thousands of caves, we strongly recommend candidate caves be investigated by researchers with expert knowledge to characterize diversity of bat species and other cave-dependent wildlife. We used only mist nets to characterize bat diversity because they are lightweight, easy to acquire and inexpensive in comparison to harp traps and acoustic detectors. While we had high capture success using mist nets alone (i.e., capturing all cave-roosting bat species on Bohol Island with the exception of one species), we encourage the use of harp traps and acoustic detectors by researchers to increase the detectability of high-frequency echolocating bat species (Flaquer et al., 2007; Francis, 1989), which in turn could influence abundance-based analyses. Although beyond the scope of our study, to maximize returns on limited financial resources available for conservation initiatives, final decisions on priority caves should consider the social, political and economic culture of the region (McBride et al., 2007).

In light of increasing human pressures on caves, many countries have put forth policies recently to conserve caves in order to maintain healthy cave ecosystems diverse in cave-dependent wildlife (e.g., Philippines, Slovenia, Puerto Rico), yet tools for prioritizing caves are lacking. Our study fills this need by identifying correlates of cave bat diversity that are readily available (i.e., open-source data) or require little time and training (i.e., cave surveys, local

resident interviews), providing an effective, easy-to-use tool to prioritize caves. Our prioritization schemes are directly applicable to other Southeast Asian countries since taxonomic congruency among species exists within the region; in addition, cave-roosting bats face similar human threats throughout (Kingston, 2010). We suggest that correlates of bat diversity can be used as a foundation for prioritizing caves globally, but we caution that differences in evolutionary history and ecological niches of bats, and the history of land-use change, in other regions warrant validation and parameterization of our correlative approach beyond Southeast Asia. Ultimately, adoption of prioritization schemes based on correlates of bat diversity could not only ensure protection of cave-roosting bat species but the subterranean biodiversity hotspots they support.

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663 Table 1. Framework for quantifying human disturbance at each cave, based on a modified version of the karst disturbance index
664 developed by van Beynen and Townsend (2005).

Scale	Indicator	3	2	1	0
Surface-level Disturbances (within 1 km)	Non-forested Habitat	> 66%	< 33%	34 – 66%	None
	Urbanization	Large city (> 1,000 residents)	Small town (100 - 1,000 residents)	Rural settlements	None
	Road Size	Major highway	Two-lane road	Single-lane trail	None
Subsurface-level Disturbances	Mining [*]	Large-scale operation (> 10%)	Moderate-scale operation (1 – 10%)	Small-scale operation (< 1%)	None
	Development	Lighting systems, paved walkways	Primitive walkways, stairs	Signage or marked trail to cave	None
	Resource Extraction ⁺	> 66%	34 – 66%	< 33%	None
	Bat Hunting ⁺	> 66%	34 – 66%	< 33%	None
	Household Waste [*]	Widespread areas (> 66%)	34 – 66%	Isolated areas (< 33%)	None
	Vandalism/Graffiti [*]	Widespread areas of graffiti or speleothem removal (> 66%)	Speleothems removed or graffiti in several areas (34 – 66%)	Isolated areas of graffiti or vandalism (< 33%)	None
	Visitation Frequency ⁺⁺	Daily	Weekly	Monthly	Never/Yearly

665 *Scoring was based on percentage of cave area impacted by the indicator; ⁺Scoring was based on percentage of interviewees that
666 responded that they or someone they knew extracted resources or hunted bats in the cave; ⁺⁺Scoring was assigned based on the highest
667 visitation frequency that two or more local residents indicated during interviews.

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682 Table 2. First six components derived from principal component analysis of environmental and human disturbance factors.

	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalues	2.33	1.54	1.38	1.21	1.06	1.00
Explained variance (%)	30.2	13.2	10.6	8.2	6.2	5.6
Interpretation	Surface-level Disturbance	Cave Complexity	Mining	Cave Development	Resource Extraction in Protected Areas	Bat Hunting
PC Loadings						
Available Roosting Area (m ²)		0.499		0.108	-0.264	-0.119
Structural heterogeneity	0.207	0.386	-0.192		-0.227	
No. Entrances	0.125	0.373	-0.157		-0.141	
Temperature Range (°C)	0.108	0.346	-0.353	0.167	0.271	
Humidity Range (%)			-0.473	-0.126	0.497	-0.180
Non-forested Habitat	0.353	-0.157				
Urbanization	0.347	-0.168	-0.154		0.173	0.100
Road Size	0.327	-0.252	-0.137			
Mining	0.214	0.132	0.405			-0.420
Cave Development	0.275			0.480		0.154
Resource Extraction		0.278	0.247	-0.466	0.356	-0.261
Bat Hunting	0.171	0.191	0.253	-0.200	0.187	0.576
Household Waste	0.268		0.302		0.101	0.365
Vandalism/Graffiti	0.278	0.150	0.243	0.234		
Visitation Frequency			0.285	0.484	0.344	-0.257
Distance to Village (km)	-0.288	0.112		0.281		
Distance to Access (km)	-0.316	0.230			0.148	0.162
Protected Area	-0.259			0.222	0.414	0.309

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684 Loadings greater than 0.30 explain a large percentage of the variance (Harlow, 2014) and are in bold.

685 Table 3. Results of *mvabund* analysis of deviance (*anova.manyglm*) (Wang et al., 2014) testing the significance of predictor variables
686 (PC1 – PC6) on assemblage composition and species abundance.

Predictor Variable	Deviance	<i>p</i> -value	Positive	Negative
Surface-level Disturbance (PC1)	39.68	0.003	<i>Myotis macrotarsus</i> <i>Rousettus amplexicaudatus</i>	<i>Emballonura alecto</i> <i>Hipposideros pygmaeus</i>
Cave Complexity (PC2)	54.45	0.020	<i>Hipposideros diadema</i> <i>Miniopterus tristis</i> <i>Rhinolophus arcuatus</i> <i>Rhinolophus philippinensis</i> <i>Rhinolophus rufus</i>	<i>Hipposideros obscurus</i>
Mining (PC3)	23.07	0.539		<i>Hipposideros ater</i>
Cave Development (PC4)	74.04	0.144	<i>Taphozous melanopogon</i>	<i>Hipposideros diadema</i>
Resource Extraction in Protected Areas (PC5)	31.75	0.509		<i>Cynopterus brachyotis</i> <i>Myotis macrotarsus</i>
Bat Hunting (PC6)	33.88	0.488	<i>Rousettus amplexicaudatus</i>	<i>Miniopterus australis</i>

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688 Significant *p*-values for predictor variables are in bold and only species with *p*-values < 0.05 in unadjusted post-hoc univariate tests
689 are shown.

Fig. 1. Caves (n = 62) surveyed on Bohol Island, Philippines (see insert). See Appendix A for detailed information about each cave.

Fig. 2. NMDS ordination biplot of species (abbreviations) with predictor variables superimposed, caves were removed to reduce clutter. The direction of each plotted arrow indicates the direction of an increase in the gradient for the corresponding variable, while the length is proportional to the correlation between the predictor variable and the ordination. Solid arrows in bold are significantly correlated with the ordination ($p < 0.05$), while dashed arrows are not. Species codes are listed in Appendix B.

Fig. 3. Number of species conserved by protecting 10% of caves ($n = 6$) based on three prioritization schemes: Scheme 1 - lowest score on PC1 (surface-level disturbance; long dash line), Scheme 2 - highest scores on PC2 (cave complexity; long dash line) and Scheme 3 - combination of the prior schemes (low surface-level disturbance and high cave complexity scores; dash-dot line). The three schemes are compared to random selection (solid black line; dotted gray lines indicate 95% confidence intervals) and selection of caves with the highest species richness (short dash line).