

# Species undersampling in tropical bat surveys: effects on emerging biodiversity patterns

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## Summary

1. Undersampling is commonplace in biodiversity surveys of species-rich tropical assemblages in which rare taxa abound, with possible repercussions for our ability to implement surveys and monitoring programmes in a cost-effective way.
2. We investigated the consequences of information loss due to species undersampling (missing subsets of species from the full species pool) in tropical bat surveys for the emerging patterns of species richness (SR) and compositional variation across sites.
3. For 27 bat assemblage data sets from across the tropics, we used correlations between original data sets and subsets with different numbers of species deleted either at random, or according to their rarity in the assemblage, to assess to what extent patterns in SR and composition in data subsets are congruent with those in the initial data set. We then examined to what degree high sample representativeness ( $r \geq 0.8$ ) was influenced by biogeographic region, sampling method, sampling effort or structural assemblage characteristics.

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4. For SR, correlations between random subsets and original data sets were strong ( $r \geq 0.8$ ) with moderate (ca. 20%) species loss. Bias associated with information loss was greater for species composition; on average ca. 90% of species in random subsets had to be retained to adequately capture among-site variation. For nonrandom subsets, removing only the rarest species (on average c. 10% of the full data set) yielded strong correlations ( $r > 0.95$ ) for both SR and composition. Eliminating greater proportions of rare species resulted in weaker correlations and large variation in the magnitude of observed correlations among data sets.

5. Species subsets that comprised ca. 85% of the original set can be considered reliable surrogates, capable of adequately revealing patterns of SR and temporal or spatial turnover in many tropical bat assemblages. Our analyses thus demonstrate the potential as well as limitations for reducing survey effort and streamlining sampling protocols, and consequently for increasing the cost-effectiveness in tropical bat surveys or monitoring programmes. The dependence of the performance of species subsets on structural assemblage characteristics (total assemblage abundance, proportion of rare species), however, underscores the importance of adaptive monitoring schemes and of establishing surrogate performance on a site by site basis based on pilot surveys.

**Key-words:** biodiversity surveys, Chiroptera, cost-effectiveness, representative sampling, species rarity, species subsamples

## Introduction

Recent studies suggest that the indicator potential and surrogacy value of single taxa is usually poor (Kessler *et al.* 2011; Larsen *et al.* 2012) and that tropical biodiversity surveys should aim to include as many different taxa as possible under given financial and logistical constraints. Selection of 'high-performance indicator taxa' for monitoring purposes requires consideration not only of the ecological value of a taxon, but also of the practical feasibility and cost-effectiveness with which it can be surveyed (Gardner *et al.* 2008; Kessler *et al.* 2011). The monetary cost and time allocation necessary to survey a given taxon, undoubtedly, are two of the main constraints faced in monitoring programmes, which therefore typically seek to obtain the information required for the least cost and within the shortest time (Gardner *et al.* 2008; McDonald-Madden *et al.* 2010).

Designing a survey programme that is at the same time statistically robust and cost-effective requires balancing opposing limitations – maximizing sample representativeness (i.e. trying to enumerate all or most species in an assemblage), vs. maximizing statistical power by increasing the number of sites surveyed at the expense of survey comprehensiveness. The effects of reducing cost and sampling effort may be particularly significant when those species that are most difficult to sample are also the rare ones. Species that are locally rare abound in species-rich assemblages in the humid tropics (e.g. Coddington *et al.* 2009), usually rendering attempts at achieving sampling completeness in biodiversity surveys or monitoring programmes cost-ineffective. Apart from species that are genuinely rare as a result of small geographic ranges, limited habitat breadth or low local population density (Rabinowitz 1981), in many cases, apparent rarity may simply

reflect a sampling artefact linked to sampling effort, methodology, or differential species detectability (Kéry & Schmid 2008; van der Burg *et al.* 2011; Meyer *et al.* 2011). As a recent study suggests, the explicit inclusion or exclusion of rare species can profoundly affect estimates of the relative conservation value of different land uses (Barlow *et al.* 2010) and can be thought to generally influence comparisons of biodiversity survey or monitoring data among habitat or land-use types.

Bats are considered potentially valuable indicators of biodiversity and ecosystem health, and there is now increased momentum for establishing a global bat-monitoring network (Jones *et al.* 2009, 2013b; Flaquer & Puig-Montserrat 2012). The value of bats as bioindicators stems from their high taxonomic and functional diversity, widespread geographic distribution, their documented sensitivity to a host of anthropogenic alterations in habitat quality and to changes in environmental conditions associated with climate change (Jones *et al.* 2009; Sherwin, Montgomery & Lundy 2013). Moreover, response patterns of bats to habitat deterioration may be congruent with those of other taxa, such as insects (Jones *et al.* 2009), an important attribute with respect to the surrogacy value of a particular taxon (Moreno *et al.* 2007). Especially, in the tropics where bats reach peak species richness (SR) and comprise a large fraction of local mammal faunas, they are providers of key ecosystem services and as such are integral to ecosystem functioning (Kalka, Smith & Kalko 2008; Lobova, Geiselman & Mori 2009; Kunz *et al.* 2011). Single localities in Neotropical lowland forests may support more than 100 sympatric bat species (Rex *et al.* 2008) and highly species-rich assemblages are also known from both tropical Asia (Kingston, Boo Liat & Zubaid 2006) and Africa (Fahr & Kalko 2011). Despite the fact that most bat biodiversity is concentrated in the

tropics, current systematic monitoring efforts focus on bats in temperate regions (Battersby 2010).

Adequate sample representativeness is a fundamental tenet of any monitoring programme or biodiversity study, as replicate surveys should adequately reflect the underlying assemblage at a site. As we have previously shown, in tropical bat surveys a certain number of repeat visits is indispensable for reliable estimation of species detectability (Meyer *et al.* 2011) and the detection of population trends (Meyer *et al.* 2010). However, as for other highly diverse tropical taxa, aiming to capture the whole spectrum of diversity at a site may not be feasible in practice as it would require a disproportionate and usually prohibitively large amount of resources within a project's given budgetary and time constraints. On the other hand, such efforts might not even be necessary when the primary objective is to characterize assemblage/environment associations or track changes in SR or turnover rather than an in-depth enumeration of all species present at a site.

The effects of excluding rare species on assemblage comparisons have been well studied and have been the subject of controversial debate for aquatic macroinvertebrate and fish assemblages (Cao, Williams & Williams 1998; Marchant 2002; Holtrop, Cao & Dolan 2010; Wan *et al.* 2010). A recent study by Vellend, Lilley & Starzomski (2008) addressed this topic also for several terrestrial taxa, including plants, reptiles, birds and alpine mammals. However, for species-rich tropical bat assemblages inferential biases associated with information loss due to species under sampling have not been systematically assessed and remain poorly understood.

Drawing from a unique suite of some of the most extensive tropical bat assemblage data sets available, pantropical in extent, our aim was to evaluate the effectiveness of species subsets in representing among-site variation in SR and composition. To this end, we assessed the magnitude of correlations for bat SR and species composition, respectively, between each full data set that included all species sampled vs. species subsets with different numbers of species deleted either at random, or according to their rarity in the respective assemblage. We predicted that species subsets would be less effective at describing among-site variation in species composition compared with SR, as found for other taxa (Magierowski & Johnson 2006; Vellend, Lilley & Starzomski 2008). Further, we expected subset performance to be dependent on (i) sampling effort and sampling method, due to their influence on species detectability (Meyer *et al.* 2011) and consequently on patterns of species rarity; (ii) structural assemblage characteristics, particularly the proportion of rare species, whereby subset performance should decrease with increasing proportions of rare species in assemblages; and (iii) biogeographic region, considering that bat assemblages in the Neotropics and Palearctica are structured differently (e.g. Struebig *et al.* 2013).

If species subsets retained sufficient information relative to full species sets and, for instance rare species that

would be time-intensive to survey could be ignored with little loss of information, survey costs may be considerably reduced, as fewer repeat visits per sampling site would be required. Our assessment therefore is of immediate relevance in the context of evaluating the feasibility and cost-effectiveness of a potential future monitoring programme for tropical bats. Moreover, our analysis is timely in view of the recently revived interest in the role of bats as bioindicators (Flaquer & Puig-Montserrat 2012).

## Materials and methods

### DATA SETS

We focused on tropical bat assemblages as this study was conceived as part of an evaluation of the suitability of tropical bats for long-term monitoring within Conservation International's Tropical Ecology, Assessment and Monitoring (TEAM) network (<http://www.teamnetwork.org>). Following a call for data among tropical bat ecologists, a total of 27 data sets were provided by colleagues and included in the study (Table S1, Supporting information). In all cases, data sets consisted of species abundance data collected at multiple sampling sites. For data sets originating from fragmented or otherwise disturbed areas, data only from control plots in continuous or mostly undisturbed forest were used for analysis. Nineteen data sets were based on ground-level mist netting (GN), six on canopy-level mist netting (CN) and two on acoustic sampling (AS). The majority of data sets were from the Neotropics (21 compared with six from the Palearctica). Disparities in the data sets' coverage reflect general differential research efforts in terms of sampling method and geographic region (e.g. Kingston 2013). Although the data sets analysed cannot be regarded as representing 100% sampled assemblages from which to subsample, they were comparable in that they comprised bat assemblages that in each case were thoroughly sampled to similarly high levels of completeness [mean inventory completeness  $81.3 \pm 6.6\%$  SD (range 67–92%)] as assessed with the Jackknife1 SR estimator; Gotelli & Colwell 2010).

### GENERATION OF RANDOM AND NONRANDOM SPECIES SUBSETS

For each data set, we calculated SR for each site. In addition, we performed a detrended correspondence analysis (DCA) based on the species by site matrix of each data set and extracted the site scores of the first DCA axis (DCA1), which represents the dominant gradient in species composition (Legendre & Legendre 1998; see Vellend, Lilley & Starzomski 2008 for details about the rationale for choosing this eigenanalysis-based ordination method in the context of the present analysis). As a measure of species composition complementary to DCA1, we calculated Jaccard's dissimilarity index ( $J$ ) for each pair of sites, one of the most widely used dissimilarity indices for species presence/absence data (Jost, Chao & Chazdon 2011).

For all data sets, we calculated SR, DCA1 and  $J$  for the full data set, that is, using the full species pool (hereafter denoted  $SR_{FULL}$ ,  $DCA1_{FULL}$  and  $J_{FULL}$ ). We then calculated SR, DCA1 and  $J$  for different subsets of species per data set ( $SR_{SUB}$ ,  $DCA1_{SUB}$  and  $J_{SUB}$ ), whereby two different approaches were taken. In the first case, species were randomly drawn from the

original species pool at each of five species pool sizes (i.e. producing five species subsets of a variable number of species). The latter ranged from 90% down to 50% of the full species pool. Following Vellend, Lilley & Starzomski (2008), at each species pool size, 100 subsets of species were randomly chosen with replacement. For each random draw of species, Pearson product-moment correlations between the full vs. randomly generated reduced data sets [ $r(\text{SUB} \times \text{FULL})$ ] were subsequently used to characterize the degree to which patterns of SR and composition in the data subsets reflect those in the complete data set. For each data set, we plotted the median and 95th percentile correlations for the 100 random subsets against species pool size. We based assessments of the effect of randomly subsampling the entire species pool on the lower 95th percentile of the 100 correlations at each species pool size, which can be regarded as a conservative estimate of the information loss as a consequence of surveying less than the full set of species (see Vellend, Lilley & Starzomski 2008).

As a second approach, in addition to evaluating the consequences of random species subsampling, we explored the effects of removing species from the full species pool in a nonrandom fashion, based on their rarity in the local assemblage. To this end, we calculated the relative abundance (RA) (%) for each species per data set and selected species subsets by eliminating increasingly larger proportions of rare species. Rare species were defined as those with a RA <1% of total RA (Maurer & McGill 2011). The average proportion of rare species across data sets was  $0.54 \pm 0.15$  (range 0.12–0.71). Depending on the species-abundance distribution of the respective assemblage, we evaluated effects with respect to up to three different rarity thresholds (whenever applicable), successively removing all species with RA <0.1%, <0.5%, and <1%, that is, always starting with the rarest species. As with random species subsets, we assessed correlations between full data sets and nonrandom subsets for SR, DCA1 and  $J$ .

We then calculated for each data set the minimum proportion of species from the full set of species that would be required to achieve lower 95th percentile correlations  $r(\text{SUB} \times \text{FULL})$  of  $\geq 0.8$ . We considered a correlation of 0.8 as an appropriate threshold as the effectiveness of using a species subset as a surrogate at lower correlation levels is questionable and may provide misleading statistical results (Vellend, Lilley & Starzomski 2008).

Analyses were conducted in R (R Development Core Team 2010), mostly using package *vegan* (Oksanen *et al.* 2008) and code adapted from Vellend, Lilley & Starzomski (2008) for generating random species subsets. Differences between response metrics, nonrandom data subsets and sampling methods in the magnitude of achieved correlations  $r(\text{SUB} \times \text{FULL})$  were tested in a linear mixed model framework in the R package *lme4* (Bates & Maechler 2010), using likelihood ratio tests to assess significance (Zuur *et al.* 2009).

#### CORRELATES OF HIGH SAMPLE REPRESENTATIVENESS

We assessed whether the surrogate effectiveness of species subsets, defined as the proportion of species necessary to reach lower 95th percentile correlations  $r \geq 0.8$ , was influenced by factors related to biogeographic region (Neotropics, Palaetropics), sampling method [GN, CN (AS was not considered as there were only two data sets)], sampling effort (number of sampling plots, mean number of surveys per sampling plot), or structural characteristics of the respective assemblage [total assemblage abundance, proportion

of rare species (those representing <1% of total RA) and the reciprocal form of Simpson's Diversity Index  $1/D$  (e.g. Maurer & McGill 2011)]. Similarly, for nonrandom species subsets with rare species removed, we modelled the probability of achieving a correlation of 0.8 between full and reduced data sets (binary response variable) as a function of those same covariates.

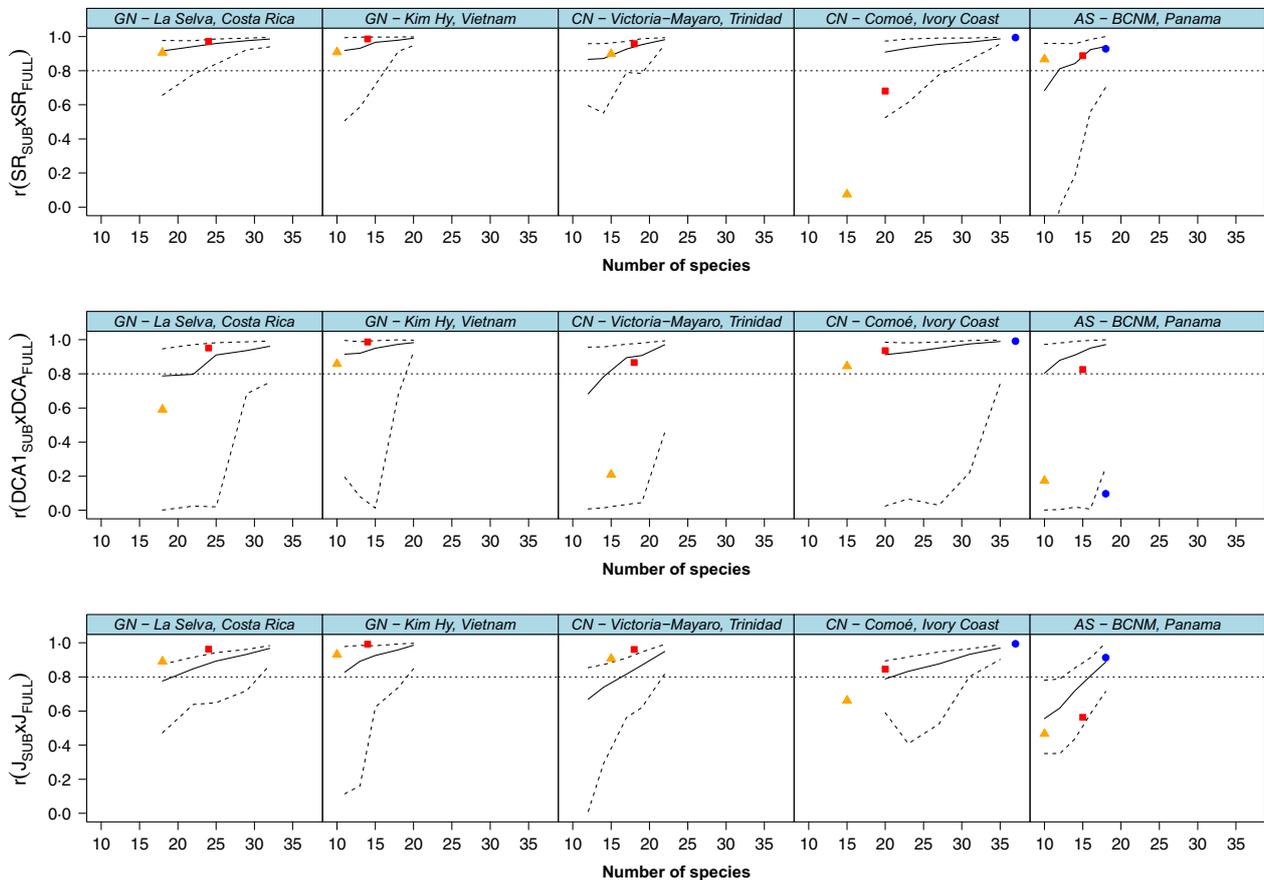
Analyses were performed as generalized linear mixed-effects models (GLMMs; Zuur *et al.* 2009), with 'location' specified as random factor. Models were fitted using the *glmer* function in the R package *lme4* (Bates & Maechler 2010), assuming a binomial error distribution and logit link function. To account for the variation in inventory completeness among data sets, we included this variable as an offset. Continuous predictor variables were standardized to facilitate comparison of parameter estimates (Schielzeth 2010). We conducted AIC<sub>c</sub>-based model selection and multimodel inference (Burnham & Anderson 2002) using the R package *AICcmodavg* (Mazerolle 2010). We chose AIC over other model selection criteria such as BIC as it is not only by far the most widely used in ecological studies, but also the best suited in the context of our application based on a recently developed decision framework (Aho, Derryberry & Peterson 2014).

## Results

### RANDOM SPECIES SUBSETS

Median correlations between full data sets and random subsets in general showed relatively little variation across data sets, and irrespective of the response metric, strong correlations were observed even with a large fraction of species removed (Figs 1, 2, S1 and S2, Supporting information). For species subsets representing 50% of the initial species pool, median correlations averaged  $0.87 \pm 0.10$  SD (range 0.64–0.98) for SR,  $0.83 \pm 0.12$  (range 0.44–0.99) for DCA1, and  $0.76 \pm 0.09$  (range 0.56–0.94) for  $J$  across all data sets analysed.

On the other hand, lower 95th percentile correlations, which represent a more conservative estimate, suggest that a great deal of information may be lost unless most of the original species set is retained. The magnitude of lower 95th percentile correlations differed significantly according to sampling method (LMM,  $\chi^2 = 7.35$ , d.f. = 2,  $P = 0.025$ ), being slightly higher for data sets based on canopy vs. ground mist netting (Tukey contrasts,  $Z = -2.51$ ,  $P_{\text{adj.}} = 0.028$ ). Moreover, it differed significantly with respect to the response metric considered ( $\chi^2 = 29.04$ , d.f. = 2,  $P < 0.001$ ), with generally weaker correlations for DCA1 compared with SR ( $Z = 4.31$ ,  $P_{\text{adj.}} < 0.001$ ) and  $J$  ( $Z = 5.06$ ,  $P_{\text{adj.}} < 0.001$ ). Correlations were weak with large proportions of the species pool dropped and highly variable among data sets, especially for DCA1 (Fig. 2); average correlations at  $\leq 70\%$  of the original species pool were <0.56 for SR, <0.27 for DCA1 and <0.55 for  $J$ . Strong lower 95th percentile correlations were only found with 90% of species retained, averaging  $0.89 \pm 0.12$  (range 0.53–0.99) for SR,  $0.64 \pm 0.30$  (range 0.11–0.99) for DCA1 and  $0.80 \pm 0.18$  (range 0.05–0.96) for  $J$  (Fig. 2). In other words, across data sets, for SR on average  $79.8 \pm 15.6\%$



**Fig. 1.** The magnitude of correlations across sites between the original data set and subsets of data for species richness (SR), and for species composition as represented by the ordination scores of the first axis of a detrended correspondence analysis (DCA1) and the Jaccard index ( $J$ ). Shown are examples for bat assemblages from both the New and Old World tropics based on ground-level mist netting (GN), canopy-level mist netting (CN) and acoustic sampling (AS). See Figs S1 and S2 (Supporting information) for plots for all data sets included in the study. Subsets were generated by deleting different numbers of species either at random or based on species rarity. The bold line connects median correlations  $r(\text{SUB} \times \text{FULL})$  for 100 randomly chosen subsets at each of five species pool sizes; the broken lines indicate upper and lower 95th percentile correlations. Open circles denote nonrandom subset correlations, with species eliminated based on up to three abundance thresholds, whenever applicable ( $RA < 0.1\%$  (●),  $< 0.5\%$  (■),  $< 1\%$  (▲)).

(range 40.9–100%) of the species from the initial set were necessary to achieve lower 95th percentile correlations  $r \geq 0.8$  between original data sets and random subsets. Effective surrogates for species composition would require that on average roughly 90% of the original species pool be retained (DCA1:  $88.8 \pm 15.8\%$ , range 51.4–100%;  $J$ :  $90.0 \pm 8.3\%$ , range 68.2–100%).

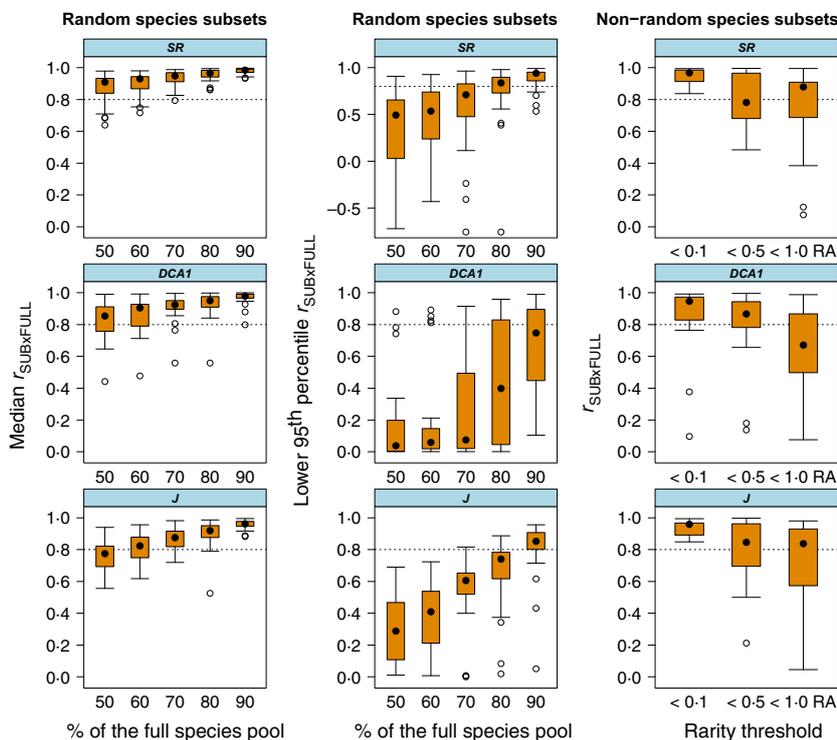
#### NONRANDOM SPECIES SUBSETS

As with random species subsampling, eliminating species from the original species pool in a nonrandom fashion based on their rarity in the respective assemblage yielded correlations that were highly variable across data sets (Figs 1, 2, S1 and S2, Supporting information). The magnitude of correlations between original and reduced data sets did not vary significantly among response metrics (LMM,  $\chi^2 = 1.75$ , d.f. = 2,  $P = 0.418$ ) or sampling methods ( $\chi^2 = 2.06$ , d.f. = 2,  $P = 0.356$ ). It did, however, differ significantly among data subsets, that is, depending on what fraction of rare species was trimmed off from the

tail of the species-abundance distribution ( $\chi^2 = 20.46$ , d.f. = 2,  $P < 0.001$ ). Irrespective of the response metric, correlations across data sets were on average  $> 0.8$  when only the rarest species ( $< 0.1\%$  of total RA, corresponding to  $9.4 \pm 11.2\%$  of the initial species pool) were eliminated, with little variation among data sets for SR and  $J$  compared with DCA1 (SR:  $0.95 \pm 0.05$ , range 0.84–0.99; DCA1:  $0.82 \pm 0.29$ , range 0.10–0.99;  $J$ :  $0.94 \pm 0.05$ , range 0.85–0.99). Additionally removing the species in the next higher rarity categories ( $< 0.5$  and  $< 1\%$  of total RA, corresponding to  $39.9 \pm 19.4\%$  and  $54.4 \pm 15.3\%$ , respectively, of the initial species pool) resulted in significantly lower correlations (Tukey contrasts,  $P_{\text{adj.}} < 0.001$ ) and increased variability in the magnitude of correlations among data sets also for SR and  $J$  (Fig. 2).

#### CORRELATES OF HIGH SAMPLE REPRESENTATIVENESS

For random species subsampling, AIC<sub>c</sub>-model selection revealed strong support for an effect of sampling effort,



**Fig. 2.** Boxplots summarizing Pearson product-moment correlations between reduced and full species sets across all data sets examined in this study. For random species subsets, provided are both median correlations as well as lower 95th percentile correlations at five different species pool sizes. For nonrandom subsets, correlations are shown for each of the three threshold levels of relative abundance (RA) based on which rare species were eliminated from the full species pool.

particularly the number of repeat visits per plot, on the proportion of species required to yield lower 95th percentile correlations  $r(\text{SUB} \times \text{FULL}) \geq 0.8$  (Tables 1 and 3). Number of surveys or the composite model 'sampling effort', which considered the number of sampling plots and the number of visits/plot, were the top-ranked or second-ranked model in the candidate set, irrespective of the response metric chosen.

In the case of nonrandom species subsets (Tables 2 and 3), for SR and  $J$  as response metrics, high sample repre-

**Table 1.** Comparative performance of GLMMs at predicting high sample representativeness for *random species subsets* based on  $AIC_c$  model selection. Models are shown up to 95% of cumulative Akaike weights ( $\omega$ ), with the ones receiving the strongest support ( $\Delta AIC_c < 2$ ) shown in bold

Subset	Model	$K$	$AIC_c$	$\Delta AIC_c$	$\omega$
Random – SR	<b>Mean no. of surveys</b>	<b>3</b>	<b>127.22</b>	<b>0</b>	<b>0.47</b>
	'Sampling effort'	4	129.91	2.69	0.12
	No. of plots	3	130.17	2.95	0.11
	Total assemblage abundance	3	130.48	3.26	0.09
	Simpson's diversity $1/D$	3	130.87	3.65	0.08
Random – DCA1	Prop. of rare species	3	131.79	4.57	0.05
	'Assemblage properties'	5	132.50	5.28	0.03
	Region	3	132.79	5.57	0.03
	<b>'Sampling effort'</b>	<b>4</b>	<b>118.64</b>	<b>0.00</b>	<b>0.83</b>
Random – $J$	<b>Mean no. of surveys</b>	<b>3</b>	<b>91.28</b>	<b>0.00</b>	<b>0.70</b>
	<b>'Sampling effort'</b>	<b>4</b>	<b>93.40</b>	<b>1.95</b>	<b>0.26</b>

DCA, detrended correspondence analysis; SR, species richness.

sentativeness was most strongly correlated with the proportion of rare species in the assemblage ( $\omega = 0.63$  and  $\omega = 0.88$ , respectively). For DCA, there was considerable evidence for an overall effect of structural assemblage characteristics, although  $AIC_c$ -differences and model weights suggested considerable model selection uncertainty. Total

**Table 2.** Comparative performance of GLMMs at predicting high sample representativeness for *nonrandom species subsets* based on  $AIC_c$  model selection. Models are given up to 95% of cumulative Akaike weights ( $\omega$ ), with the ones receiving the strongest support ( $\Delta AIC_c < 2$ ) shown in bold

Subset	Model	$K$	$AIC_c$	$\Delta AIC_c$	$\omega$
Nonrandom – SR	<b>Prop. of rare species</b>	<b>3</b>	<b>27.07</b>	<b>0</b>	<b>0.63</b>
	Simpson's diversity $1/D$	3	30.67	3.60	0.10
	Mean no. of surveys	3	31.43	4.36	0.07
	Total assemblage abundance	3	32.55	5.48	0.04
	Region	3	32.66	5.59	0.04
	Method	3	32.69	5.62	0.04
	No. of plots	3	32.76	5.69	0.04
Nonrandom – DCA1	<b>Total assemblage abundance</b>	<b>3</b>	<b>34.05</b>	<b>0</b>	<b>0.31</b>
	<b>Simpson's diversity <math>1/D</math></b>	<b>3</b>	<b>35.03</b>	<b>0.98</b>	<b>0.19</b>
	<b>Prop. of rare species</b>	<b>3</b>	<b>35.56</b>	<b>1.51</b>	<b>0.14</b>
	Region	3	36.61	2.56	0.09
	No. of plots	3	36.61	2.56	0.09
	Mean no. of surveys	3	36.77	2.72	0.08
	Method	3	36.79	2.74	0.08
Nonrandom – $J$	<b>Prop. of rare species</b>	<b>3</b>	<b>19.07</b>	<b>0.00</b>	<b>0.88</b>
	'Assemblage properties'	5	23.17	4.11	0.11

**Table 3.** Model-averaged parameter estimates, unconditional standard errors and 95% confidence intervals for the best-selected GLMM models ( $\Delta\text{AIC}_c < 2$ ) assessing correlates of high sample representativeness for random and nonrandom species subsets

Subset	Model	Estimate	SE	95% unconditional CI	
				Lower	Upper
Random – SR	Mean no. of surveys	0.58	0.26	0.07	1.10
Random – DCA1	Mean no. of surveys	1.55	0.49	0.59	2.51
	No. of plots	1.65	0.64	0.40	2.89
Random – <i>J</i>	Mean no. of surveys	0.60	0.20	0.21	0.98
	No. of plots	0.16	0.17	–0.18	0.49
Nonrandom – SR	Prop. of rare species	–1.74	0.92	–3.54	0.05
Nonrandom – DCA1	Total assemblage abundance	–0.83	0.57	–1.96	0.29
	Simpson's $1/D$	0.65	0.57	–0.47	1.76
	Prop. of rare species	–0.69	0.76	–2.17	0.79
Nonrandom – <i>J</i>	Prop. of rare species	–6.76	3.90	–14.4	0.89

DCA, detrended correspondence analysis; SR, species richness.

assemblage abundance was the top-ranked model ( $\omega = 0.31$ ), followed by Simpson's diversity index ( $\omega = 0.19$ ) and the proportion of rare species ( $\omega = 0.14$ ).

## Discussion

We quantified inferential biases associated with species subsampling in tropical bat assemblages and demonstrate that moderately undersampled species subsets may in many cases be sufficient to enable reliable comparisons of SR and compositional variation across sites. As expected, species subsets performed better at retaining information on intersite variation in SR than species composition. Moreover, in line with our predictions, we found that sampling effort and structural assemblage characteristics, specifically the proportion of rare species in an assemblage, were important predictors of subset performance. In contrast, there was no significant effect of either sampling method or geographic region on high sample representativeness.

### SURROGATE PERFORMANCE OF RANDOM AND NONRANDOM SUBSETS

Similar assessments for a diverse array of other taxa, including plants, invertebrates, fish, reptiles, birds and nonvolant mammals (Vellend, Lilley & Starzomski 2008; Molloy *et al.* 2010; Bried *et al.* 2012) also found high levels of congruence between full and reduced data sets when ignoring 10%, and often larger proportions, of the original species pool. Our results show that information loss was equally low with similar levels of species' exclusion (ca. 15%). An important caveat to note is that our analysis was based on data sets that had an average of 81% completeness. Although we statistically controlled for variation in inventory completeness among data sets in modelling correlates of high sample representativeness, it remains unknown to what degree our results might have been different if we had subsampled fully inventoried

assemblages, that is, data sets that had near 100% completeness.

In many instances, we found that correlations for nonrandom subsets mirrored those based on random subsets reasonably well; however, for certain data sets, correlations deviated considerably from median correlations for randomly chosen subsets. Strong differences were particularly apparent with DCA1 correlations for some data sets (e.g. Comoé, Yungas, Victoria-Mayaro, Fig. S1b, Supporting information), whereas agreement between correlations for random and nonrandom subsets was in most cases much better for SR and *J*. Our findings concur with those of Vellend, Lilley & Starzomski (2008) in that correlations for DCA1 often showed greater variability across data sets than for *J*. This indicates that species subsets may often be less effective at capturing the same maximum possible amount of compositional variation among sites (as given by DCA1) than the full set. In contrast, pairwise site differences (Jaccard dissimilarities) in species composition may be more consistently revealed with a reasonably large subsample of the entire species set.

While part of our analyses focused on random species subsets, our findings concerning the effects of undersampling due to species rarity for predicting diversity patterns may be more revealing and of greater general relevance. Corroborating previous studies on invertebrates (Heino & Soininen 2010; Franklin *et al.* 2013), our results suggest that patterns of spatial turnover in tropical bat assemblages are to a large extent driven by the more common species and for the accurate description of assemblage similarity-environment relationships, rare species may often be of limited importance. Removing only the least abundant species from an assemblage (those with <0.1% of total RA, comprising on average *c.* 10% of the original species pool) yielded strong correlations (>0.8) across nearly all data sets (Fig. 2). This indicates that if only the rarest species in an assemblage were missed during a survey, information loss would be tolerable in most cases and that the species subset sampled can serve as a good

surrogate for the full suite of species actually present in the assemblage. Limiting surveys to sampling only the more common species and ignoring the rarest ones therefore seems a reasonable shortcut for reducing costs in tropical bat monitoring programs. It is important, however, to emphasize that our findings in this regard do not apply to situations where the objective is the detailed population monitoring of rare species. Although inherently of greater conservation interest than common ones, rare species in tropical bat assemblages are difficult to monitor and will always require a high-effort sampling design for reliable trend detection, as we have previously demonstrated (Meyer *et al.* 2010). Common species have variously been shown to contribute disproportionately to SR patterns (Pearman & Weber 2007; Gaston 2008; Šizling *et al.* 2009; Lennon *et al.* 2011). Our results are in line with these findings and point towards a considerable degree of structural redundancy in species composition (*sensu* Clarke & Warwick 1998) in tropical bat assemblages, which may in fact be a general feature of many biological communities (Cayuela, De La Cruz & Ruokolainen 2011).

#### FACTORS AFFECTING SPECIES SUBSET PERFORMANCE

Contrary to expectations, subset performance was not dependent on geographic region. However, this finding should be interpreted with some caution as our study included far more data sets from the New World than from the Old World tropics, which may have reduced statistical power to detect significant differences. Only increased research efforts underway in Asia (Kingston 2013) and, hopefully, in the future also in Africa, can help to substantiate this finding based on a geographically more balanced set of studies.

While sampling effort was the best correlate of high sample representativeness with random subsampling, structural assemblage characteristics, most notably the proportion of rare species in an assemblage, was the best predictor of surrogate performance when data sets were subsampled according to rarity. Tropical bat assemblages typically comprise many rare species, yet vary substantially with respect to the number of rare species they contain, as evidenced by our data sets (Fig. 3). Our results imply that whenever assemblages are comprised of a large number of rare species, relatively larger fractions of these will need to be sampled to adequately capture among-site variation in SR and composition, essentially requiring increased sampling effort and more comprehensive surveys. Trimming off progressively greater proportions of species (i.e. species representing <0.5 and <1% of total RA, encompassing on average 40% and 54%, respectively, of the full set) resulted in correlations often lower than 0.8 (Fig. 2). Correlations <0.7 may greatly reduce the statistical power for testing relationships between species diversity or composition and environmental

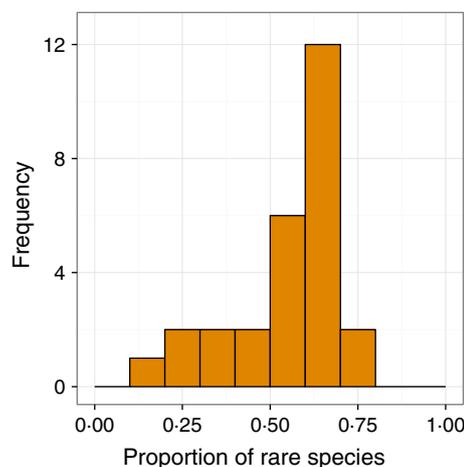


Fig. 3. Frequency histogram of the proportion of rare species across the data sets analysed.

covariates, and in fact, only strong relationships may be detectable using a surrogate in such cases (Vellend, Lilley & Starzomski 2008). Thus, in the search for suitable surrogates, correlations >0.7 should be aimed for to guarantee that assemblage-environment relationships can be reliably assessed.

That inferential biases associated with undersampling increase for species-rich assemblages that are made up of a large number of rare species can clearly be seen in the case of the assemblages from Comoé (Ivory Coast), Victoria-Mayaro (Trinidad) or Barro Colorado Nature Monument (Panama), each characterized by a high proportion of rare species (60–70%). Congruence in multivariate response patterns between original data and subsets with all of those rare species removed was generally very low (correlations  $\ll$  0.8), particularly for DCA1. For these assemblages, subsets containing only the more abundant species would fail to capture the same dominant gradient in species composition as in the initial data set. This was most prominent in the Comoé ground-net assemblage where even removing only the rarest few species yielded a correlation of <0.4 (Fig. S1b, Supporting information). Such apparent failure to capture among-site patterns in species composition with species subsets may reflect the major role of high habitat heterogeneity in shaping diversity patterns in this particular assemblage. The Comoé assemblage had the largest proportion of rare species of all data sets examined (71%) and is characterized by high SR, a pattern largely attributable to its geographical position in a biome transition zone between forest and savanna, where habitat heterogeneity is sharply elevated (Fahr & Kalko 2011). In contrast, the bat assemblage at Tiputini (Ecuador), although one of the most species-rich known (Rex *et al.* 2008), is characterized by comparatively higher evenness of its abundance distribution, which may explain the generally high correlations found with nonrandom species removal. These findings indicate that the trade-off between number of sites surveyed and survey

comprehensiveness is system-specific. This in turn implies that the investment required for capturing a representative sample of the whole assemblage varies across geographic locations, reflecting spatial variation in the number of rare species and ultimately in mean species detection probabilities (Meyer *et al.* 2011), both of which are intuitively closely linked (McCarthy *et al.* 2013). Gauging the relationship between species abundance and detectability is important as it can help to determine adequate sampling effort. However, in general, how exactly detection probabilities scale with abundance remains little explored (McCarthy *et al.* 2013), an aspect which provides an interesting avenue for future research in the context of bat biodiversity surveys.

The majority of assemblages analysed in this study were sampled using a single method, ground-level mist nets, reflecting the general fact that tropical bat assemblage inventories that use a combination of different survey methods remain scarce. Our low sample size for data sets not based on ground-level mist netting may in part explain why, opposite to what we expected, sampling method was not found to be an important predictor of species subset performance. Sampling method influences species detectability in tropical bats (Meyer *et al.* 2011) and hence is an important determinant of local-scale patterns of species rarity. To accurately infer which species in an assemblage are truly rare therefore requires comprehensive surveys employing a combination of active (i.e. mist netting at ground- and canopy level, harp traps) and passive survey methods (AS) to maximize inventory completeness (MacSwiney, Clarke & Racey 2008; Kunz, Hodgkinson & Weise 2009; Kingston 2013). Consequently, assessments of the surrogate effectiveness of species subsets should ideally be based on assemblages that have been surveyed with multiple complementary methods to properly account for confounding effects of sampling method on patterns of species rarity. If we had had such data available, this would no doubt have strengthened the robustness of our inferences drawn about how the exclusion of rare species influences surrogate effectiveness. We therefore consider this an important aspect that merits attention in similar future evaluations.

#### SURROGATE EFFECTIVENESS OF SPECIES SUBSETS: SPECIES RICHNESS VS. COMPOSITION

As predicted and corroborating previous work on other taxa (Magierowski & Johnson 2006; Vellend, Lilley & Starzomski 2008), we found that partial species sets generally are robust surrogates of total SR; however, they perform less well in uncovering compositional patterns. Although SR is a state variable commonly used in monitoring programmes (Jones *et al.* 2013a), its usefulness in environmental impact assessments has recently been questioned as measures of assemblage composition and turnover have been found to be more informative and sensitive to change (Barlow *et al.* 2007; Magurran &

Henderson 2010; Banks-Leite, Ewers & Metzger 2012; Dornelas *et al.* 2014). Undersampling bias is a key challenge not only with regard to biodiversity assessment and monitoring, as examined here, but also constitutes an active area of research in many other fields of ecological research, including species distribution modelling (Kramer-Schadt *et al.* 2013; Syfert, Smith & Coomes 2013) or the analysis of plant-animal interaction networks (Nielsen & Bascompte 2007; Rivera-Hutinel *et al.* 2012), where equivalents of SR (e.g. interaction richness) have also been found to be less robust than alternative metrics (e.g. Tylianakis *et al.* 2010). This highlights the general need for ecologists and conservation biologists to move beyond mere species numbers and to focus on more informative assemblage metrics, capable of adequately capturing changes in relation to environmental impacts or monitoring alterations in ecological network structure. We argue that in the context of monitoring for environmental impact assessment researchers should give greater consideration to measures of species composition and turnover to increase the validity of inferences made from evaluations of the suitability and performance of species subsets as surrogates of total taxon richness. More specifically, we advocate a wider application of metrics suitable for quantifying biodiversity change, for instance commonly applied similarity or distance measures (e.g. the Morisita–Horn Index) and specialized turnover indices (Magurran & Henderson 2010; Jost, Chao & Chazdon 2011; Magurran 2011) or rank abundance statistics such as mean rank shift (Collins *et al.* 2008). The merits and necessity of a shift of focus towards such measures are well illustrated by the recent finding of a global analysis of long-term assemblage time series, which detected no systematic temporal change in alpha diversity, but consistent compositional change and turnover (Dornelas *et al.* 2014).

#### Conclusions

Our analyses stress that there is potential for reducing costs in tropical bat monitoring by streamlining sampling activities if the focus is on assessing assemblage–environment relationships or changes in SR or turnover. Protocols that consider reasonably high but not exhaustive sampling, which may equate to fewer surveys, seem to be sufficiently sensitive to allow reliable inferences regarding among-site variation in bat SR and assemblage composition. This suggests that survey efficiency may be maximized by ignoring those species that are most time-consuming to sample, that is, those that make up the far end of the extended rare species tail of the relative species-abundance distribution.

Our analyses demonstrate, however, that a one-size-fits-all approach to surrogate selection based on species subsets may be inappropriate but will have to be tailored to site-specific circumstances and consider the structural idiosyncrasies of local assemblages. In essence, monitoring programmes will have to establish site-specific

performance levels for biodiversity surrogates based on pilot data. In practice, this will require relatively detailed surveys at the beginning of a survey or monitoring programme, which should entail the use of multiple sampling methods to accurately establish true patterns of species rarity. Such pilot surveys should be combined with the application of robust statistical approaches to assess survey completeness based on the SR estimator most appropriate for a given data set (see Reese, Wilson & Flather 2014 for a recent framework concerning estimator selection) to determine to what extent the use of species subsets is justifiable (Franklin *et al.* 2013). Implementing adaptive sampling schemes that avoid oversampling at some sites and undersampling at others (cf. Holtrop, Cao & Dolan 2010), that is, aim to spatially prioritize sampling effort, may ultimately be key to maximizing cost-effectiveness in tropical bat surveys. Finally, when adopting a surrogate as part of a bat monitoring programme or in environmental impact assessments it will be essential to assess its robustness across relevant spatial and also temporal scales, and to determine its performance prior to and after environmental impact as disturbance may alter the relationship between the species subset and total biodiversity (Magie-rowski & Johnson 2006; Sebek *et al.* 2012).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Table S1.** List of data sets used in this study.

**Fig. S1.** Plots showing correlations between full and reduced data sets based on ground-level mist netting.

**Fig. S2.** Plots showing correlations between full and reduced data sets based on canopy-level mist netting and acoustic sampling.