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 programs 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 and compositional variation across sites.

3. For 27 bat assemblage datasets from across the tropics, we used correlations between original datasets 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 species richness and composition in data subsets are congruent with those in the initial dataset. 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.

4. For species richness, correlations between random subsets and original datasets 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 non-random subsets, removing only the rarest species (on average ~10% of the full dataset) yielded strong correlations ($r > 0.95$) for both species richness and composition. Eliminating greater proportions of rare species resulted in weaker correlations and large variation in the magnitude of observed correlations among datasets.

5. Species subsets that comprised ca. 85% of the original set can be considered reliable surrogates, capable of adequately revealing patterns of species richness 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 programs. 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 programs, 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 program 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), versus 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 programs 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 artifact linked to sampling effort, methodology, or differential species detectability (Kéry & Schmid 2008; Meyer *et al.* 2011; van der Burg *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; Flaquer & Puig-Montserrat 2012; KE Jones *et al.* 2013). 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 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 program 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 species richness 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 undersampling have not been systematically assessed and remain poorly understood.

Drawing from a unique suite of some of the most extensive tropical bat assemblage datasets available, pantropical in extent, our aim was to evaluate the effectiveness of species subsets in representing among-site variation in species richness and composition. To this end, we assessed the magnitude of correlations for bat species richness and species composition, respectively, between each full dataset 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 to species richness, as found for other taxa (Magierowski & Johnson 2006; Vellend *et al.* 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 Paleotropics 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 program 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

DATASETS

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 datasets were provided by colleagues and included in the study (Table S1, Supporting Information). In all cases, datasets consisted of species abundance data collected at multiple sampling sites. For datasets originating from fragmented or otherwise disturbed areas, data only from control plots in continuous or mostly undisturbed forest were used for analysis. Nineteen datasets were based on ground-level mist netting (GN), six on canopy-level mist netting (CN), and two on acoustic sampling (AS). The majority of datasets were from the Neotropics (21 compared to six from the Paleotropics). Disparities in the datasets' coverage reflect general differential research efforts in terms of sampling method and geographic region (e.g. Kingston 2013). Although the datasets 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 ± 6.6% SD [range 67-92%] as assessed with the Jackknife1 species richness estimator; Gotelli & Colwell 2010).

GENERATION OF RANDOM AND NON-RANDOM SPECIES SUBSETS

For each dataset, we calculated species richness (SR) for each site. In addition, we performed a detrended correspondence analysis (DCA) based on the species-by-site matrix of each dataset and extracted the site scores of the first DCA axis (DCA1), which represents the dominant gradient in species composition (Legendre & Legendre 1998; see Vellend *et al.* 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 datasets, we calculated SR, DCA1 and J for the full dataset, i.e. using the full species pool (hereafter denoted $\mathrm{SR}_{\mathrm{FULL}}$, $\mathrm{DCA1}_{\mathrm{FULL}}$, and J_{FULL}). We then calculated SR, DCA1, and J for different subsets of species per dataset ($\mathrm{SR}_{\mathrm{SUB}}$, $\mathrm{DCA1}_{\mathrm{SUB}}$, 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 *et al*. (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 datasets [r(SUB x FULL)] were subsequently used to characterize the degree to which patterns of species richness and composition in the data subsets reflect those in the complete dataset. For each dataset, we plotted the median and 95$^{\mathrm{th}}$

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 *et al.* 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 non-random fashion, based on their rarity in the local assemblage. To this end, we calculated the relative abundance (RA) (%) for each species per dataset and selected species subsets by eliminating increasingly larger proportions of rare species. Rare species were defined as those with a relative abundance less than 1% of total relative abundance (Maurer & McGill 2011). The average proportion of rare species across datasets was 0.54 ± 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%, i.e. always starting with the rarest species. As with random species subsets, we assessed correlations between full datasets and non-random subsets for SR, DCA1, and *J*.

We then calculated for each dataset the minimum proportion of species from the full set of species that would be required to achieve lower 95th percentile correlations r(SUB x FULL) of ≥ 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 *et al.* 2008).

Analyses were conducted in R (R Development Core Team 2010), mostly using package vegan (Oksanen *et al.* 2008) and code adapted from Vellend *et al.* (2008) for generating random species subsets. Differences between response metrics, non-random data subsets, and sampling methods in the magnitude of achieved correlations *r*(SUB x 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, Palaeotropics), sampling method (GN, CN [AS was not considered as there were only two datasets]), 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 non-random species subsets with rare species removed, we modeled the probability of achieving a correlation of 0.8 between full and reduced datasets (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 datasets (see above), we included this variable as an offset. Continuous predictor variables were standardized to facilitate comparison of parameter estimates (Schielzeth 2010). We conducted AIC$_c$-based model selection and multi-model 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 datasets and random subsets in general showed relatively little variation across datasets, and irrespective of the response metric, strong correlations were observed even with a large fraction of species removed (Figs 1 & 2, Figs S1 & S2). For species subsets representing 50% of the initial species pool, median correlations averaged 0.87 ± 0.10 SD (range 0.64-0.98) for SR, 0.83 ± 0.12 (range 0.44-0.99) for DCA1, and 0.76 ± 0.09 (range 0.56-0.94) for J across all datasets analyzed.

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, $\chi^2 = 7.35$, df = 2, $P = 0.025$), being slightly higher for datasets based on canopy versus ground mist netting (Tukey contrasts, $Z = -2.51$, $P_{adj.} = 0.028$). Moreover, it differed significantly with respect to the response metric considered ($\chi^2 = 29.04$, df = 2, $P < 0.001$), with generally weaker correlations for DCA1 compared to SR ($Z = 4.31$, $P_{adj.} < 0.001$) and J ($Z = 5.06$, $P_{adj.} < 0.001$). Correlations were weak with large proportions of the species pool dropped and highly variable among datasets, especially for DCA1 (Fig. 2); average correlations at ≤ 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 ± 0.12 (range 0.53-0.99) for SR, 0.64 ± 0.30 (range 0.11-0.99) for DCA1, and 0.80 ± 0.18 (range 0.05-0.96) for *J* (Fig. 2). In other words, across datasets, for SR on average 79.8 ± 15.6% (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 datasets 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 ± 15.8%, range 51.4 - 100%; *J*: 90.0 ± 8.3%, range 68.2 – 100%).

NON-RANDOM SPECIES SUBSETS

As with random species subsampling, eliminating species from the original species pool in a non-random fashion based on their rarity in the respective assemblage yielded correlations that were highly variable across datasets (Figs 1 & 2, Figs S1 & S2). The magnitude of correlations between original and reduced datasets did not vary significantly among response metrics (LMM, $\chi^2 = 1.75$, df = 2, $P = 0.418$) or sampling methods ($\chi^2 = 2.06$, df = 2, $P = 0.356$). It did, however, differ significantly among data subsets, i.e. depending on what fraction of rare species was trimmed off from the tail of the species-abundance distribution ($\chi^2 = 20.46$, df = 2, $P < 0.001$). Irrespective of the response metric, correlations across datasets were on average > 0.8 when only the rarest species (< 0.1% of total RA, corresponding to 9.4 ± 11.2% of the initial species pool) were eliminated, with little variation among datasets for SR and *J* compared to DCA1 (SR: 0.95 ± 0.05, range 0.84-0.99; DCA1: 0.82 ± 0.29, range 0.10-0.99; *J*: 0.94 ± 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 ± 19.4% and 54.4 ± 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 datasets also for SR and J (Fig. 2).

CORRELATES OF HIGH SAMPLE REPRESENTATIVENESS

For random species subsampling, AIC_c-model selection revealed strong support for an effect of sampling effort, particularly the number of repeat visits per plot, on the proportion of species required to yield lower 95th percentile correlations $r(\text{SUB x FULL}) \geq 0.8$ (Table 1 & 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 non-random species subsets (Table 2 & 3), for SR and J as response metrics, high sample representativeness 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 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 species richness and compositional variation across sites. As expected, species subsets performed better at retaining information on inter-site variation in species richness 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 NON-RANDOM SUBSETS

Similar assessments for a diverse array of other taxa, including plants, invertebrates, fish, reptiles, birds, and non-volant mammals (Vellend *et al.* 2008; Molloy *et al.* 2010; Bried *et al.* 2012) also found high levels of congruence between full and reduced datasets 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 datasets that had an average of 81% completeness. Although we statistically controlled for variation in inventory completeness among datasets in modeling correlates of high sample representativeness, it remains unknown to what degree our results might have been different if we had subsampled fully inventoried assemblages, i.e. datasets that had near 100% completeness.

In many instances we found that correlations for non-random subsets mirrored those based on random subsets reasonably well; however, for certain datasets correlations deviated considerably from median correlations for randomly chosen subsets. Strong differences were particularly apparent with DCA1 correlations for some datasets (e.g. Comoé, Yungas, Victoria-Mayaro, Fig. S1b), whereas agreement between correlations for random and non-random subsets was in most cases much better for SR and *J*. Our findings concur with those of Vellend *et al*. (2008) in that correlations for DCA1 often showed greater variability across datasets 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 ~10% of the original species pool) yielded strong correlations (> 0.8) across nearly all datasets (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 species richness 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 since our study included far more datasets 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 datasets 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 datasets (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 species richness 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 covariates, and in fact only strong relationships may be detectable using a surrogate in such cases (Vellend *et al.* 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 << 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 dataset. This was most prominent in the Comoé ground-net assemblage where even removing only the rarest few species yielded a correlation of less than 0.4 (Fig. S1b). 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 datasets examined (71%) and is characterized by high species richness, 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 non-random 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 analyzed 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 datasets 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 (acoustic sampling) to maximize inventory completeness (MacSwiney, Clarke & Racey 2008; Kunz, Hodgkison & 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 (see above). 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 *et al.* 2008), we found that partial species sets generally are robust surrogates of total species richness, however, they perform less well in uncovering compositional patterns. Although species richness is a state variable commonly used in monitoring programs (JPG Jones *et al.* 2013), 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 modeling

(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 species richness (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 *et al.* 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 species richness 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 species richness and assemblage composition. This suggests that survey efficiency may be maximized by ignoring those species that are most time-consuming to sample, i.e. 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 programs 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 program, 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 species richness estimator most appropriate for a given dataset (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 *et al.* 2010), i.e. 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 program 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 (Magierowski & Johnson 2006; Sebek *et al.* 2012).

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References

Aho, K., Derryberry, D. & Peterson, T. (2014) Model selection for ecologists: the worldviews of AIC and BIC. *Ecology,* **95,** 631-636.

Banks-Leite, C., Ewers, R.M. & Metzger, J.P. (2012) Unraveling the drivers of community dissimilarity and species extinction in fragmented landscapes. *Ecology,* **93,** 2560-2569.

Barlow, J., Gardner, T.A., Araujo, I.S., Avila-Pires, T.C., Bonaldo, A.B., Costa, J.E. *et al.* (2007) Quantifying the biodiversity value of tropical primary, secondary and plantation forest. *Proceedings of the National Academy of Sciences USA*, **104,** 18555-18560.

Barlow, J., Gardner, T.A., Louzada, J. & Peres, C.A. (2010) Measuring the conservation value of tropical primary forests: the effect of occasional species on estimates of biodiversity uniqueness. *PLoS ONE,* **5,** e9609.

Bates, D. & Maechler, M. (2010) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-999337. http://CRAN.R-project.org/package=lme999374.

Battersby, J. (2010) *Guidelines for surveillance and monitoring of European bats*. UNEP/EUROBATS Secretariat, Bonn, Germany.

Bried, J.T., Hager, B.J., Hunt, P.D., Fox, J.N., Jensen, H.J. & Vowels, K.M. (2012) Bias of reduced-effort community surveys for adult Odonata of lentic waters. *Insect Conservation and Diversity,* **5,** 213-222.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and inference: a practical information-theoretic approach,* 2nd edn. Springer, New York.

Cao, Y., Williams, D.D. & Williams, N.E. (1998) How important are rare species in aquatic community ecology and bioassessment? *Limnology and Oceanography,* **43,** 1403-1409.

Cayuela, L., De La Cruz, M. & Ruokolainen, K. (2011) A method to incorporate the effect of taxonomic uncertainty on multivariate analyses of ecological data. *Ecography,* **34,** 94-102.

Clarke, K.R. & Warwick, R.M. (1998) Quantifying structural redundancy in ecological communities. *Oecologia*, **113,** 278-289.

Coddington, J.A., Agnarsson, I., Miller, J.A., Kuntner, M. & Hormiga, G. (2009) Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. *Journal of Animal Ecology*, **78,** 573-584.

Collins, S.L., Suding, K.N., Cleland, E.E., Batty, M., Pennings, S.C., Gross, K.L. *et al.* (2008) Rank clocks and plant community dynamics. *Ecology,* **89,** 3534-3541.

Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. *et al.* (2014) Assemblage time series reveal biodiversity change but not systematic loss. *Science*, **344,** 296-299.

Fahr, J. & Kalko, E.K.V. (2011) Biome transitions as centres of diversity: habitat heterogeneity and diversity patterns of West African bat assemblages across spatial scales. *Ecography*, **34,** 177-195.

Flaquer, C. & Puig-Montserrat, X. (2012) Proceedings of the International Symposium on the Importance of Bats as Bioindicators. Museum of Natural Sciences Edicions, Granollers, Catalonia, Spain.

Franklin, E., de Moraes, J., Landeiro, V.L., de Souza, J.L.P., Pequeno, P.A.l.C.L., Magnusson, W.E. *et al.* (2013) Geographic position of sample grid and removal of uncommon species affect multivariate analyses of diverse assemblages: The case of oribatid mites (Acari: Oribatida). *Ecological Indicators,* **34,** 172-180.

Gardner, T.A., Barlow, J., Araujo, I.S., Avila-Pires, T.C., Bonaldo, A.B., Costa, J.E. *et al.* (2008) The cost effectiveness of biodiversity surveys in tropical forests. *Ecology Letters*, **11,** 139-150.

Gaston, K.J. (2008) Biodiversity and extinction: the importance of being common. *Progress in Physical Geography,* **32,** 73-79.

Gotelli, N.J. & Colwell, R.K. (2010) Estimating species richness. *Biological diversity: Frontiers in measurement and assessment* (eds A.E. Magurran & B.J. McGill), pp. 39-54. Oxford University Press.

Heino, J. & Soininen, J. (2010) Are common species sufficient in describing turnover in aquatic metacommunities along environmental and spatial gradients? *Limnology and Oceanography,* **55,** 2397-2402.

Holtrop, A.M., Cao, Y. & Dolan, C.R. (2010) Estimating sampling effort required for characterizing species richness and site-to-site similarity in fish assemblage surveys of wadeable Illinois streams. *Transactions of the American Fisheries Society*, **139,** 1421-1435.

Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R. & Racey, P.A. (2009) *Carpe noctem*: the importance of bats as bioindicators. *Endangered Species Research,* **8,** 93-115.

Jones, J.P.G., Asner, G.P., Butchart, S.H.M. & Karanth, K.U. (2013) The ‘why’, ‘what’ and ‘how’ of monitoring for conservation. *Key Topics in Conservation Biology 2* (eds D.W. Macdonald & K.J. Willis), pp. 327-343. John Wiley & Sons, Oxford, UK.

Jones, K.E., Russ, J.A., Bashta, A.-T., Bilhari, Z., Catto, C., Csősz, I. *et al.* (2013) Indicator Bats Program: a system for the global acoustic monitoring of bats. *Biodiversity Monitoring and Conservation* (eds B. Collen, N. Pettorelli, J.E.M. Baillie & S.M. Durant), pp. 211-247. Wiley-Blackwell, Oxford, UK.

Jost, L., Chao, A. & Chazdon, R.L. (2011) Compositional similarity and beta diversity. *Biological diversity: frontiers in measurement and assessment* (eds A.E. Magurran & B.J. McGill), pp. 66-84. Oxford University Press, New York.

Kalka, M.B., Smith, A.R. & Kalko, E.K.V. (2008) Bats limit arthropods and herbivory in a tropical forest. *Science,* **320,** 71.

Kéry, M. & Schmid, B.R. (2008) Imperfect detection and its consequences for monitoring for conservation. *Community Ecology,* **9,** 207-216.

Kessler, M., Abrahamczyk, S., Bos, M., Buchori, D., Putra, D.D., Robbert Gradstein, S. *et al.* (2011) Cost-effectiveness of plant and animal biodiversity indicators in tropical forest and agroforest habitats. *Journal of Applied Ecology,* **48,** 330-339.

Kingston, T., Boo Liat, L. & Zubaid, A. (2006) *Bats of Krau Wildlife Reserve*. Penerbit Universiti Kebangsaan Malaysia Press, Bangi.

Kingston, T. (2013) Response of bat diversity to forest disturbance in Southeast Asia: insights from long-term research in Malaysia. *Bat Evolution, Ecology, and Conservation* (eds R.A. Adams & S.C. Pedersen), pp. 169-185. Springer New York.

Kramer-Schadt, S., Niedballa, J., Pilgrim, J.D., Schröder, B., Lindenborn, J., Reinfelder, V. *et al.* (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions,* **19,** 1366-1379.

Kunz, T.H., Hodgkison, R. & Weise, C.D. (2009) Methods of capturing and handling bats. *Ecological and behavioral methods for the study of bats* (eds T.H. Kunz & S. Parsons), pp. 3-35. Johns Hopkins University Press, Baltimore, Maryland.

Kunz, T.H., de Torrez, E.B., Bauer, D., Lobova, T. & Fleming, T.H. (2011) Ecosystem services provided by bats. *Annals of the New York Academy of Sciences,* **1223,** 1-38.

Larsen, F.W., Bladt, J., Balmford, A. & Rahbek, C. (2012) Birds as biodiversity surrogates: will supplementing birds with other taxa improve effectiveness? *Journal of Applied Ecology*, **49,** 349-356.

Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2nd edn. Elsevier, Amsterdam.

Lennon, J.J., Beale, C.M., Reid, C.L., Kent, M. & Pakeman, R.J. (2011) Are richness patterns of common and rare species equally well explained by environmental variables? *Ecography*, **34,** 529-539.

Lobova, T.A., Geiselman, C.K. & Mori, S.A. (2009) *Seed dispersal by bats in the Neotropics*. New York Botanical Garden Press, New York.

MacSwiney, M.C., Clarke, F.M. & Racey, P.A. (2008) What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. *Journal of Applied Ecology*, **45,** 1364-1371.

Magierowski, R.H. & Johnson, C.R. (2006) Robustness of surrogates of biodiversity in marine benthic communities. *Ecological Applications*, **16,** 2264-2275.

Magurran, A.E. & Henderson, P.A. (2010) Temporal turnover and the maintenance of diversity in ecological assemblages. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365,** 3611-3620.

Magurran, A.E. (2011) Measuring biological diversity in time (and space). *Biological diversity: frontiers in measurement and assessment* (eds A.E. Magurran & B.J. McGill), pp. 85-93. Oxford University Press, New York.

Marchant, R. (2002) Do rare species have any place in multivariate analysis for bioassessment? *Journal of the North American Benthological Society*, **21,** 311-313.

Maurer, B.A. & McGill, B.J. (2011) Measurement of species diversity. *Biological diversity: frontiers in measurement and assessment* (eds A.E. Magurran & B.J. McGill), pp. 55-65. Oxford University Press, New York.

Mazerolle, M.J. (2010) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 1.13. http://CRAN.R-project.org/package=AICcmodavg.

McCarthy, M.A., Moore, J.L., Morris, W.K., Parris, K.M., Garrard, G.E., Vesk, P.A. *et al.* (2013) The influence of abundance on detectability. *Oikos,* **122,** 717-726.

McDonald-Madden, E., Baxter, P.W.J., Fuller, R.A., Martin, T.G., Game, E.T., Montambault, J. *et al.* (2010) Monitoring does not always count. *Trends in Ecology & Evolution,* **25,** 547-550.

Meyer, C.F.J., Aguiar, L.M.S., Aguirre, L.F., Baumgarten, J., Clarke, F.M., Cosson, J.-F. *et al.* (2010) Long-term monitoring of tropical bats for anthropogenic impact assessment: gauging the statistical power to detect population change. *Biological Conservation,* **143,** 2797-2807.

Meyer, C.F.J., Aguiar, L.M.S., Aguirre, L.F., Baumgarten, J., Clarke, F.M., Cosson, J.-F. *et al.* (2011) Accounting for detectability improves estimates of species richness in tropical bat surveys. *Journal of Applied Ecology,* **48,** 777-787.

Molloy, P.P., Anticamara, J.A., Rist, J.L. & Vincent, A.C.J. (2010) Frugal conservation: What does it take to detect changes in fish populations? *Biological Conservation,* **143,** 2532-2542.

Moreno, C.E., Pineda, E., Escobar, F. & Sánchez-Rojas, G. (2007) Shortcuts for biodiversity evaluation: a review of terminology and recommendations for the use of target groups, bioindicators and surrogates. *International Journal of Environment and Health,* **1,** 71-86.

Nielsen, A. & Bascompte, J. (2007) Ecological networks, nestedness and sampling effort. *Journal of Ecology,* **95,** 1134-1141.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Stevens, M.H.H. *et al.* (2008) vegan: Community Ecology Package. R package version 1.13-11. http://CRAN.R-project.org/package=vegan.

Pearman, P.B. & Weber, D. (2007) Common species determine richness patterns in biodiversity indicator taxa. *Biological Conservation,* **138,** 109-119.

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-900007-900050, http://www.R-project.org.

Rabinowitz, D. (1981) Seven forms of rarity. *The biological aspects of rare plant conservation* (ed. H. Synge), pp. 205-217. Wiley.

Reese, G.C., Wilson, K.R. & Flather, C.H. (2014) Performance of species richness estimators across assemblage types and survey parameters. *Global Ecology and Biogeography*, **23,** 585-594.

Rex, K., Kelm, D.H., Wiesner, K., Kunz, T.H. & Voigt, C.C. (2008) Species richness and structure of three Neotropical bat assemblages. *Biological Journal of the Linnean Society,* **94,** 617-629.

Rivera-Hutinel, A., Bustamante, R.O., Marín, V.H. & Medel, R. (2012) Effects of sampling completeness on the structure of plant-pollinator networks. *Ecology,* **93,** 1593-1603.

Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution,* **1,** 103-113.

Sebek, P., Barnouin, T., Brin, A., Brustel, H., Dufrêne, M., Gosselin, F. *et al.* (2012) A test for assessment of saproxylic beetle biodiversity using subsets of "monitoring species". *Ecological Indicators,* **20,** 304-315.

Sherwin, H.A., Montgomery, W.I. & Lundy, M.G. (2013) The impact and implications of climate change for bats. *Mammal Review,* **43,** 171-182.

Šizling, A., Šizlingová, E., Storch, D., Reif, J. & Gaston, K.J. (2009) Rarity, commonness, and the contribution of individual species to species richness patterns. *The American Naturalist,* **174,** 82-93.

Struebig, M.J., Turner, A., Giles, E., Lasmana, F., Tollington, S., Bernard, H. *et al.* (2013) Quantifying the biodiversity value of repeatedly logged rainforests: gradient and comparative approaches from Borneo. *Advances in Ecological Research* (eds W. Guy & J.O.G. Eoin), pp. 183-224. Academic Press.

Syfert, M.M., Smith, M.J. & Coomes, D.A. (2013) The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS ONE,* **8,** e55158.

Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010) Conservation of species interaction networks. *Biological Conservation,* **143,** 2270-2279.

van der Burg, M.P., Bly, B., VerCauteren, T. & Tyre, A.J. (2011) Making better sense of monitoring data from low density species using a spatially explicit modelling approach. *Journal of Applied Ecology,* **48,** 47-55.

Vellend, M., Lilley, P.L. & Starzomski, B.M. (2008) Using subsets of species in biodiversity surveys. *Journal of Applied Ecology,* **45,** 161-169.

Wan, H., Chizinski, C.J., Dolph, C.L., Vondracek, B. & Wilson, B.N. (2010) The impact of rare taxa on a fish index of biotic integrity. *Ecological Indicators,* **10,** 781-788.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R.* Springer, New York.

Supporting information

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

Table S1. List of datasets used in this study.

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

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

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 (ω), with the ones receiving the strongest support ($\Delta\mathrm{AIC}_c < 2$) shown in bold.

Subset	Model	K	AIC_c	$\Delta\mathrm{AIC}_c$	ω
Random – SR	**Mean no. of surveys**	**3**	**127.22**	**0**	**0.47**
	‘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
	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
Random – DCA1	**‘Sampling effort’**	**4**	**118.64**	**0.00**	**0.83**
	Mean no. of surveys	3	122.02	3.37	0.15
Random – *J*	**Mean no. of surveys**	**3**	**91.28**	**0.00**	**0.70**
	‘Sampling effort’	**4**	**93.40**	**1.95**	**0.26**

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

Subset	Model	K	AIC_c	ΔAIC_c	ω
Nonrandom – SR	**Prop. of rare species**	**3**	**27.07**	**0**	**0.63**
	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	**Total assemblage abundance**	**3**	**34.05**	**0**	**0.31**
	Simpson's diversity 1/*D*	**3**	**35.03**	**0.98**	**0.19**
	Prop. of rare species	**3**	**35.56**	**1.51**	**0.14**
	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*	**Prop. of rare species**	**3**	**19.07**	**0.00**	**0.88**
	'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 ($\Delta AIC_c < 2$) assessing correlates of high sample representativeness for random and non-random 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 – *J*	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 – *J*	Prop. of rare species	-6.76	3.90	-14.4	0.89

Figure captions

Fig. 1. The magnitude of correlations across sites between the original dataset 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 for plots for all datasets 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*(Sub x 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 non-random subset correlations, with species eliminated based on up to three abundance thresholds, whenever applicable (RA < 0.1% (●), < 0.5% (■), < 1% (▲)).

Fig. 2. Boxplots summarizing Pearson product-moment correlations between reduced and full species sets across all datasets 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 non-random 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.

Fig. 3. Frequency histogram of the proportion of rare species across the datasets analyzed.

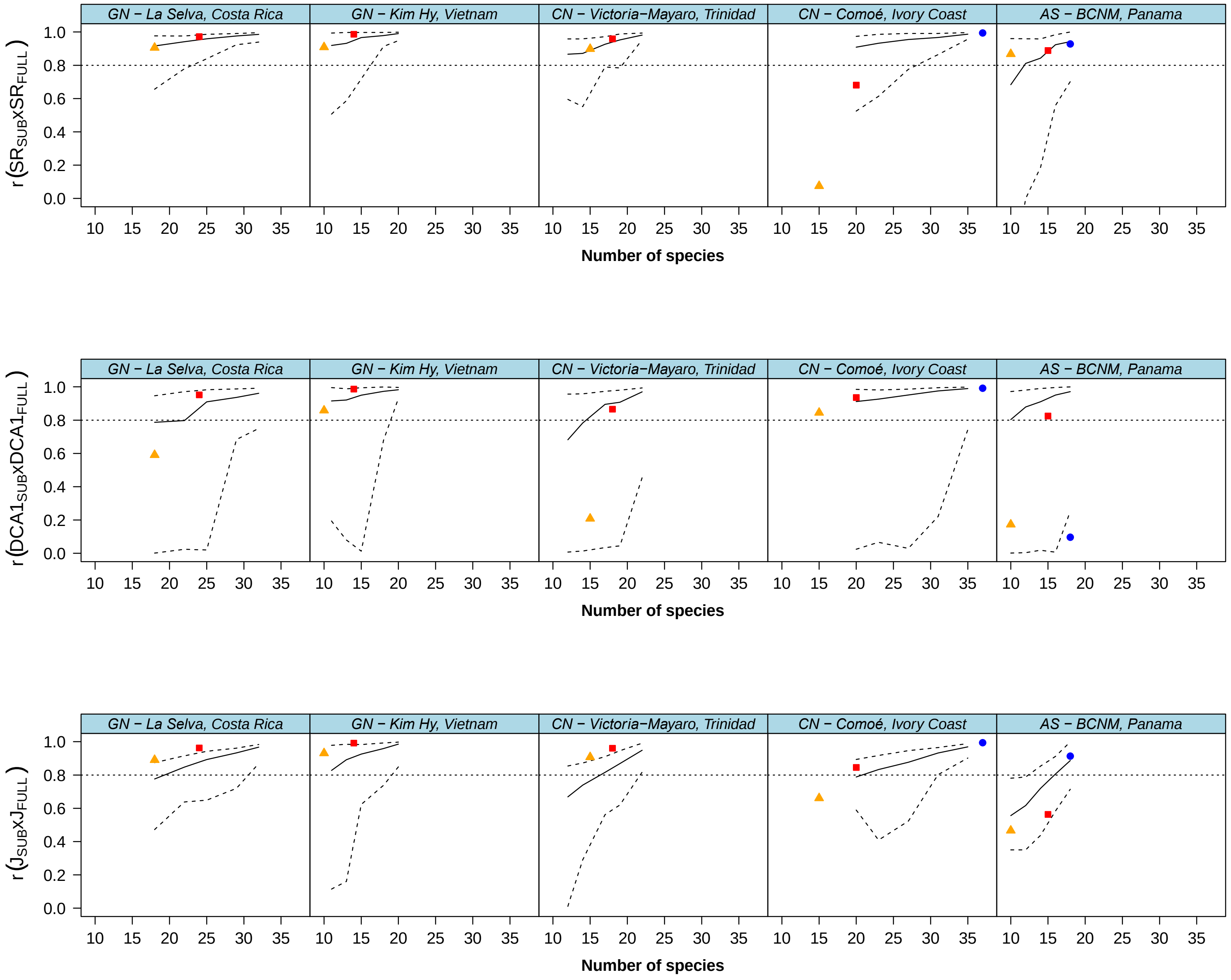
GN − La Selva, Costa Rica
GN − Kim Hy, Vietnam
CN − Victoria−Mayaro, Trinidad
CN − Comoé, Ivory Coast
AS − BCNM, Panama
$r(SR_{SUB}xSR_{FULL})$
$r(DCA1_{SUB}xDCA1_{FULL})$
$r(J_{SUB}xJ_{FULL})$
0.0
0.2
0.4
0.6
0.8
1.0
10
15
20
25
30
35
Number of species

Fig. 1

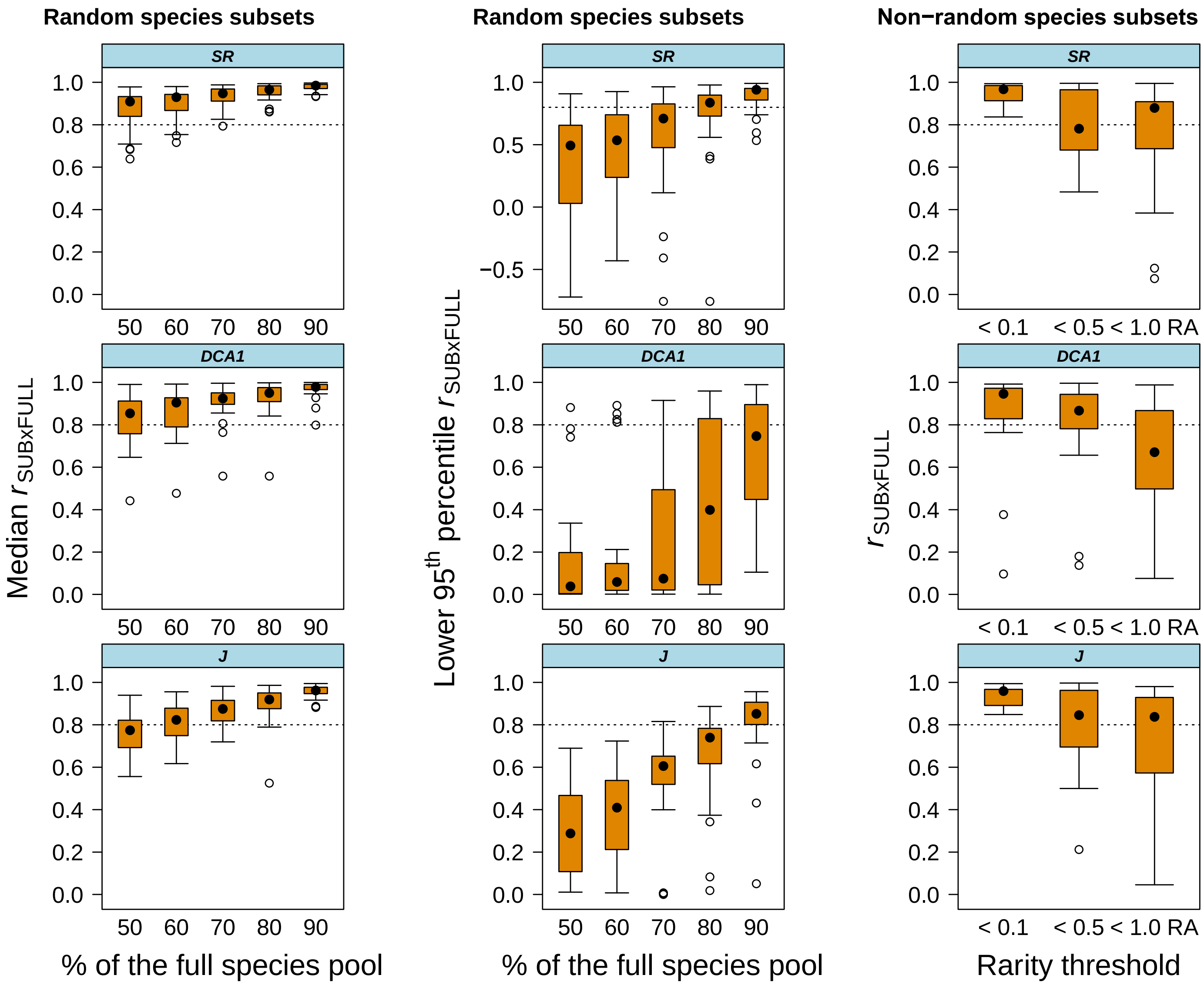
Random species subsets
Random species subsets
Non−random species subsets
SR
DCA1
J
Median r_{SUBxFULL}
Lower 95th percentile r_{SUBxFULL}
r_{SUBxFULL}
1.0
0.8
0.6
0.4
0.2
0.0
0.5
−0.5
50 60 70 80 90
< 0.1 < 0.5 < 1.0 RA
% of the full species pool
% of the full species pool
Rarity threshold

Fig. 2.

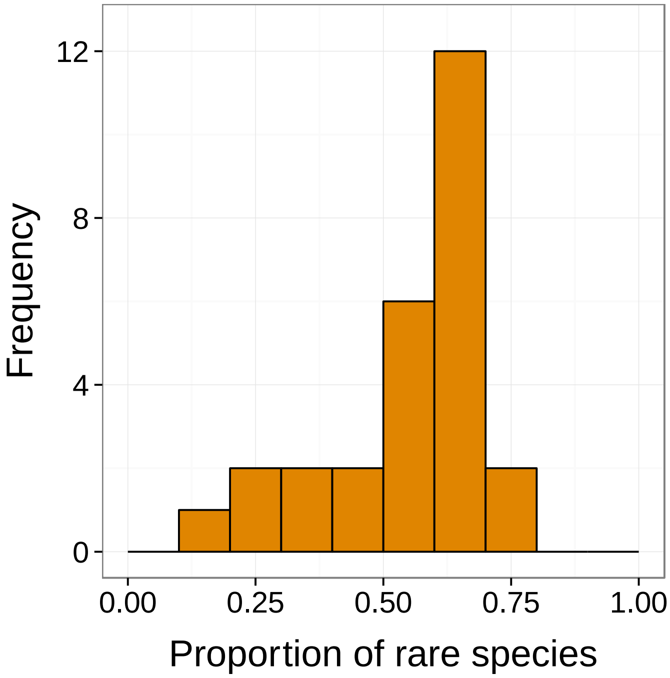
12
8
4
0
Frequency
0.00
0.25
0.50
0.75
1.00
Proportion of rare species

Fig. 3.