Incomplete sampling of geographic ranges weakens or reverses the positive relationship between an animal species' geographic range size and its body size

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ABSTRACT

Aim: To study the effects of the sampling regime on body size/range size correlations among species.

Background: Body size/range size correlations tend to be positive if geographic sampling includes all or most of the geographic area of each species in a study. However, correlations tend to be negative or non-significant if geographic sampling is only partial.

Methods: Using computer bootstrapping, we randomly sampled latitudinal ranges of 1317 species of New World mammals. We sampled along lines of fixed longitude. We studied the effects of three variables: (1) the comprehensiveness of the sample as a proportion of the entire latitudinal range; (2) the number of isolated populations within a species range; (3) the correlation of body size and range size in the computerized data set from which the samples come. The latter is termed 'weak' when we used the empirical body size and range size data. It was termed 'strong' when we replaced the real body sizes with ones assigned to produce a correlation of one with range size.

Results: Studies using incomplete ranges yield unpredictable results that might not even get the sign of the relationship correct. The unpredictability arises because incomplete sampling tends to understate the range sizes of species with the largest ranges and miss the smallest ranges entirely. Those unusual range sizes determine the true body size/range size correlation. The unpredictability worsens as more and more locations within a range lack a population, thus increasing the probability that species will be missed by an incomplete sample. The degree of unpredictability caused by incomplete sampling and the number of isolated populations did not differ between the 'weak' and 'strong' data sets.

Keywords: body size, latitude, mammals, partial sampling, range size.

INTRODUCTION

The relationships between the geographic range size and body size of phylogenetically similar animals are typically positive and linear when both variables are log-transformed

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(Brown, 1995). Many mechanisms have been hypothesized to explain this relationship, including the minimum viable population size of species [where large-bodied species may have larger home ranges (Brown and Maurer, 1987)], homeostatic and environmental variabilities [where species of large body size are able to maintain homeostasis over a wider range of environmental conditions (Gaston, 1990; Root, 1991)], and latitudinal gradients [where average body sizes and geographic range sizes of species in assemblages both tend to decline towards lower latitudes (Pagel *et al.*, 1991)]. However, a recent synthesis of range size/body size relationships of various animal groups, including mantis shrimp, insects, birds and primates, clearly illustrated that many such relationships are non-significant or negative (Gaston and Blackburn, 1996), thus warranting deeper investigation of the causes of such disparities between current hypotheses and empirical patterns.

In their study, Gaston and Blackburn (1996) showed that the 'comprehensive' analysis of range size and body size tended to result in positive relationships, whereas 'partial' analysis was more likely to result in a negative or non-significant relationship. Comprehensive studies are performed over areas which encompass most of the geographic ranges of the focal species, and partial studies are performed over areas which encompass the entire geographic ranges of none or very few of the focal species. Indeed, in a study of Afro-tropical dung beetles, Cambefort (1994) reported a clear switch from a negative to a positive range size/body size relationship driven by a change from a partial to a comprehensive analysis. Because logistical constraints often hamper a macroecologist's ability to comprehensively investigate large-ranging groups of animals, it is important that the consequences of undertaking partial investigations are quantified.

Negative or non-significant relationships resulting from partial analyses of range size/body size relationships are likely to be the product of two sampling artifacts. First, if the spatial scale of a partial analysis is small relative to the range limits of the species under study, then the ranges of larger ranging species will be truncated and smaller ranging species may be missed altogether (Gaston and Blackburn, 1996; Gaston, 2003). Second, if larger ranging and larger-bodied species occur at lower densities (Damuth, 1981, 1987), and/or form more sparsely spaced populations (Brown, 1995; Brown *et al.*, 1996), they are more likely to be missed in partial samples. Despite widespread agreement that such sampling biases may lead to weakened and potentially negative range size/body size relationships (Gaston and Blackburn, 1996; Gaston, 2003), these ideas have never been formally quantified and thus the magnitude of their effects is largely unknown.

We tested how a study's spatial scale and the distribution of populations across a geographic range affect range size/body size relationships using latitudinal ranges of 1317 extant species of New World mammals. Our aims were twofold: (1) to examine how the range size/body size relationship changes in relation to the spatial scale of the study, and (2) to examine how spatial patchiness in species distributions further changes this relationship. As a first step, we assumed that a species' body size was equivalent to its range size. This assesses the maximum potential for deterioration of the range size/body size relationship caused by sampling artifacts. If a sampling regime had no effect on the underlying relationship, any correlation test would result in unity. Because body size/range size relationships are never perfect, we then repeated our analysis using the true mammal body sizes. We expected that the effects of sampling artifacts would be more prominent when the underlying relationship was stronger. We show that, even with a perfect underlying relationship between range size and body size, these two sampling biases substantially weaken the observed relationships, and negative relationships become progressively more common for

single realizations when species are patchy and sparse over their range. Moreover, we show that these results are due to a biased loss of species in specific parts of the range size frequency distribution and not a simple loss of species due to reduced spatial scale.

MATERIALS AND METHODS

Range endpoints were collected for New World mammals using the digital distribution maps of Patterson *et al*. (2003). Only continental species were used. Average adult body mass for each species was taken from a compilation of mammalian body sizes (Smith *et al.*, 2003). Data on all extant species shared by the data sets were compiled and their ranges were standardized whereby the distance between the northernmost species occurrence and the southernmost species occurrence was equal to one (Fig. 1). In total, our data set included 1317 extant species from the mammalian orders Artiodactyla, Carnivora, Chiroptera, Didelphimorphia, Insectivora, Lagomorpha, Microbiotheria, Paucituberculata, Peris-sodactyla, Primates, Rodentia and Xenarthra. We assigned species body sizes in two ways. First, to assess the maximum divergence from a strong underlying relationship caused by sampling artifacts, the body size of each species was simply assigned as that species' total range size (i.e. we assumed *a priori* that a perfect relationship exists under a perfect sampling regime). Second, to assess how sampling artifacts affect the true underlying relationship of the mammal data, which was weak in this case (i.e. Spearman's tau = 0.1), the body size of each species was assigned its average adult mass as recovered from the literature (Smith *et al.*, 2003).

The two data sets were then sub-sampled at several spatial scales. Scales ranged from 5% of the domain or 'high partiality' to 100% of the domain or 'comprehensive', where the domain was the latitudinal range of the New World. Sub-samples were placed randomly onto the domain, and the range of each species was constrained to be the portion that fell within the sub-sample (e.g. dashed box in Fig. 1). The species' sampled range sizes were then correlated with their associated body sizes. Because resulting range size/body size relation-ships often differed from normal bivariate, Spearman's non-parametric rank correlation index, tau, was used to assess relationship strength. The sampling process was repeated 1000 times for each sub-sample size (5, 20, 50, 80 and 100% of the latitudinal domain), the resulting correlation indices ranked, and the median (the 500th rank) and 95% confidence ranges (the 25th and 975th rank) were reported. Similarly, the median and 95% confidence ranges of the number of species found within a sub-sample were reported as a proportion of the total number of species in the data set.

Because individuals or populations are not distributed continuously over their range, we evaluated the effects of partial sampling on the range size/body size relationship when 'isolates' (individuals or populations, depending of the specific animal group's ecology and a study's spatial extent) are patchy. To model the probability of sampling success within the geographic range, different numbers of isolates were randomly placed within the species' ranges. Because the most common way to measure latitudinal range is the distance between the most extreme populations, we ensured that an isolate occurred at each edge of any given geographic range (Fig. 1c). Moreover, a researcher performing a partial study is constrained to define a species range size using the most distant populations within the study area. If the vertical line in Fig. 1c represents the range of a species and the circles represent where isolates are actually found over this range, it is easy to see that the range recorded by a partial sub-sample (dashed box) will be severely underestimated. This result is primarily due
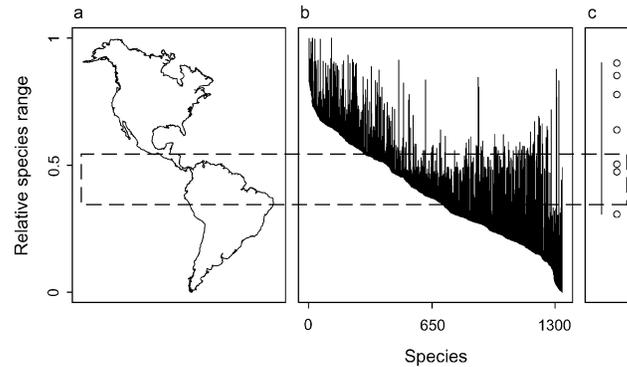
Fig. 1. (a) Map of North and South America (the New World); (b) the corresponding latitudinal ranges for each of the 1317 extant mammal species in the New World Mammal Database (solid vertical lines). Panel (c) illustrates the differences between partial sampling of a continuous range (solid line) and a range within which species clump in discrete isolates (open circles, representing populations or individuals depending on the spatial scale of the study).

to the fact that the maximum possible range size will be determined by the sub-sample size, and secondarily that a low number of isolates will likely decrease the observed range size further or miss that species altogether. If only one isolate was sampled, a range size could not be calculated and it was therefore removed from the analysis of that sub-sample.

Evidence suggests that the abundances of individuals or populations tend to be higher at the centre of their geographic range (Brown *et al.*, 1995), although these patterns are not always straightforward (Gilbert, 1980; Rapoport, 1982; Carter and Prince, 1985; Thomas *et al.*, 1998; Blackburn *et al.*, 1999). Therefore, placement of isolates over each range was done using both uniform and normal probability density distributions with $\mu = 0$, $\sigma = 1$ scaled for each species' range. The number of isolates over each species' geographic range varied from two (i.e. where isolates occur only at the range edges) to continuous (i.e. where isolates occur everywhere over the range). By maintaining an equal number of isolates within each species' geographic range, larger ranging species (and, thus as hypothesized, larger-bodied species) would subsequently have lower isolate densities in accordance with Damuth's (1981, 1987) observed pattern. To avoid making assumptions about the spatial extent of populations for different species, isolates were modelled as infinitesimal points on a species' range. In practice, the position of isolates and the partial samples were chosen using a random number generator to eight decimal points.

The number of species sampled naturally decreases with increasing sub-sample partiality and decreasing number of isolates per range. We performed an additional set of simulations because we expect these sampling artifacts to affect specific areas of the range size/body size relationship (i.e. we expect the missing species to be a non-random sample of the total). Because the effect of number of isolates per range on the number of species sampled was small (see Results), the additional simulations were performed assuming continuous isolates. For each run of the simulation, we drew the same number of species that were intercepted by a sub-sample randomly from the full data set without replacement. If the range size of the randomly sampled species was greater than the level of partiality would allow, the range size was truncated to the size of the partial sub-sample. This rule was

imposed for two reasons. First, a randomization that does not truncate species ranges to the scale imposed by sampling partiality will converge on the results of a comprehensive sample. For example, randomly sampling from the perfect data set, where range size and body size are equal, will always result in a correlation of one. Second, because partiality causes ranges to be truncated, it is more realistic to include this rule in the randomizations. Correlation coefficients were calculated for the randomly sampled range sizes and the corresponding body sizes. The median and 95% confidence limits were compared with those generated in the original simulations described above.

RESULTS

This study clearly demonstrated the way in which two ubiquitous sampling artifacts in macroecological studies, sampling partiality and population patchiness, can potentially affect the strength of range size/body size relationships. As expected, average reductions in observed relationship strength were especially obvious when the real underlying relationship was strong (Fig. 2a), with these disparities being less prominent when the underlying relationship was weak (Fig. 2b).

Sample partiality

In all cases, as partiality increases, the variation in the estimated correlation coefficient increases (Fig. 2a,b). These trends occur whether the underlying 'true' relationship is strong (Fig. 2a) or weak (Fig. 2b). However, when the underlying relationship is strong, the median correlation of the 1000 simulations decreases with increased partiality (Fig. 2a). In contrast, when the underlying relationship is weak, the effect on the median is small (Fig. 2b).

Isolates per range

The different random distributions of isolates between range edges (i.e. uniform densities and a range of plausible normal densities) had trivial effects on the results and the differences are not reported here. The results using the uniform distribution are represented in Fig. 2a,b. The amount of variation in the estimated correlation coefficient increased with decreased number of isolates regardless of whether the underlying relationship was strong or weak (Fig. 2a,b). However, when the underlying relationship was weak, the estimated median was similar regardless of the number of isolates per range (Fig. 2b). This was not the case when the underlying relationship was strong. The estimated median was farther from the true value at lower numbers of isolates (Fig. 2a).

Sample size

The number of species sub-sampled decreases with increasing sample partiality and decreasing number of isolates (Fig. 2c). This was the same whether the underlying relationship was strong or weak because these sampling artifacts affect only the range size of a species, regardless of its body mass. The effect of sample partiality on number of species was greater than that of the number of isolates (Fig. 2c, compare the differences among different symbols with the differences among the same symbols). Note that the median proportion of species sub-sampled decreases more rapidly as sampling partiality increases at a given number of isolates than it does when number of isolates decreases at a
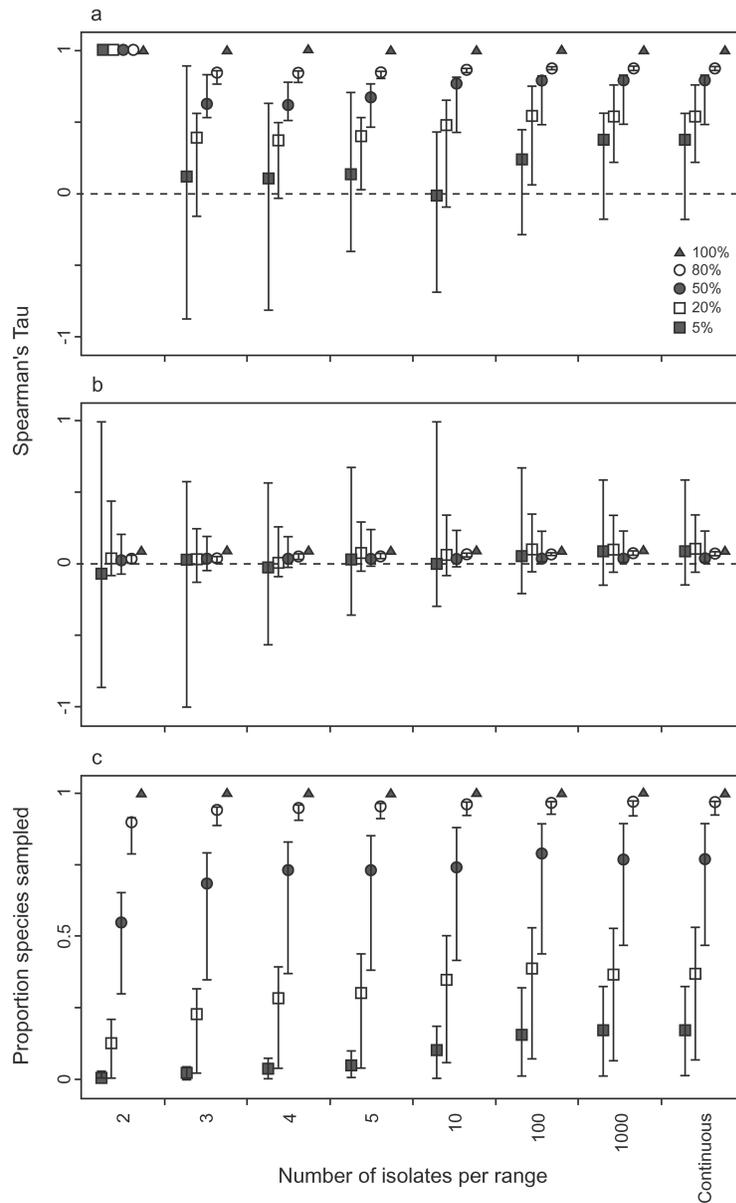
Fig. 2. A graphical representation of the weakening relationship between range size and body size for New World mammals as a function of sampling partiality and number of isolates within a given species range. Panel (a) shows the analysis when assuming that body size is equal to range size – representing a strong underlying relationship. Panel (b) shows the analysis when real mammal body size estimates are used – representing a weak underlying relationship. Presented are the medians for five different degrees of sampling partiality (5, 20, 50, 80 and 100%) and the corresponding 95% confidence ranges – a measure of the statistical uncertainty for each realization of a given sample. The number of isolates (the x-axis) ranged from two, where only the endpoints of a species range were considered, through to continuous over a species range. Panel (c) shows the median proportion of the total species intercepted by a sub-sample for each combination of isolate number and sampling partiality and the corresponding 95% confidence ranges.

given level of partiality. Indeed, the proportion of species sub-sampled remains relatively constant, at each level of partiality, until the number of isolates is 10 or lower.

We found, however, that the loss of species due to sampling artifacts was non-random (Fig. 3) because species were missed from specific parts of the range size frequency distribution (Fig. 4). If the underlying relationship was strong, randomly sub-sampling
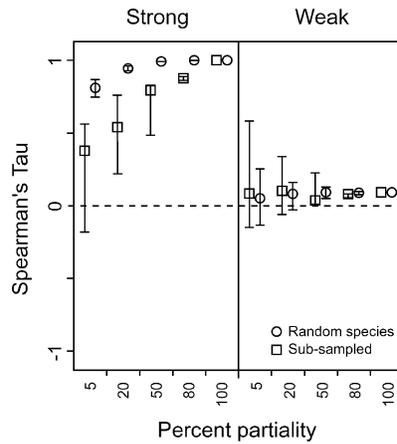

Fig. 3. A graphical representation of the difference between the estimated correlation coefficients and 95% confidence ranges under the sub-sampling regime shown in Fig. 2 (open squares) and a random sub-sampling regime (open circles). Simulations were run using both a strong (left-hand side of the graph) and a weak (right-hand side of the graph) underlying relationship. Isolates were continuous and all levels of partiality were examined.
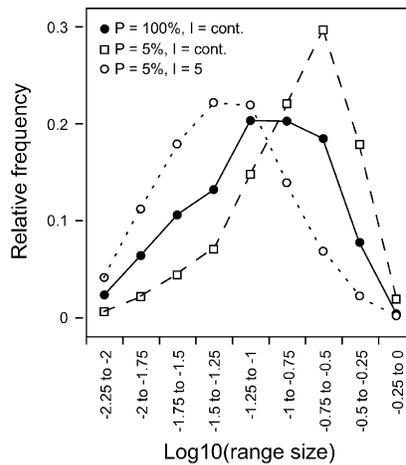

Fig. 4. A graphical representation of the relative range size frequency distributions for different combinations of sub-sample partiality (P) and isolate number (I). Closed circles represent the relative proportions of species whose log latitudinal ranges fall within each bin when sub-sampling is comprehensive (P = 100%) and isolates are continuous (I = cont.). Squares represent the relative proportions of species whose log latitudinal ranges fall within each bin when sub-sampling is highly partial (P = 5%) and isolates are continuous (I = cont.). Finally, open circles encompass the situation when partiality is high (P = 5%) and number of isolates is low (I = 5).

species resulted in markedly higher correlation coefficients than resulted from the sampling artifacts [Fig 3, compare circles (random sampling) with squares (sampling artifacts)]. If the underlying relationship was weak, the resulting correlation coefficients were similar (Fig. 3). However, the variation in estimated correlation coefficients was much greater when the loss of species was due to sampling artifacts (Fig. 3, compare confidence limits of circles with those of squares). Therefore, regardless of the underlying range size/body size relationship, randomly sampling from the species pool will do a better job of estimating the underlying range size/body size relationship than sampling a randomly selected geographic area.

The non-random effects of these sampling artifacts can be illustrated by comparing the relative frequency distribution for the real range sizes of the species within a partial sub-sample with the relative range size frequency distribution for the complete data set (Fig. 4). We used more extreme levels of partiality and isolate numbers (e.g. 5% partiality, 5 isolates) to better illustrate the effects on the species that are sub-sampled. Because we were interested in examining the range sizes of missing species, we plotted the true range sizes of the species intercepted by the simulations rather than the truncated range sizes. When isolates are continuous, but sampling partiality is at 5%, the loss of species occurs disproportionately on the left-hand side of the range size frequency distribution (Fig. 4, compare solid circles with squares). However, when the number of isolates is 5 and sampling partiality is at 5%, additional species are lost from the right-hand side of the range size frequency distribution (Fig. 4, contrast solid circles with open circles). If the loss of species were random, the relative frequency distributions resulting when the sampling artifacts are acting should approximately overlap that of the full data set (Fig. 4, solid circles).

DISCUSSION

One common and often unavoidable artifact in macroecological studies is partiality of sampling, in which broad-scale relationships are inferred from data that are collected at scales that do not fully encapsulate a variable of interest – a widespread example being species range sizes (Gaston *et al.*, 1996; Gaston and Blackburn, 1996). In the case of the relationship between range size and body size of animals, it has been shown that partial studies are more prone to non-significant or negative correlations than are comprehensive studies (Gaston and Blackburn, 1996). We confirm this claim quantitatively. By not sampling the full geographic range of a group of species, the association between range size and body size becomes weaker (Fig. 2a,b). More importantly, however, is that a partial sub-sample (which represents a single empirical study) is unpredictable with respect to the true underlying relationship.

There were two mechanisms by which sampling partiality weakened the range size/body size relationship. First, because the maximum possible range of a species was constrained by the sub-sample size, sampling partiality disproportionately truncated the ranges of larger ranging species. Second, the number of species sampled decreased in concert with increased sub-sample partiality (Fig. 2c). However, although decreased sample size alone would reduce confidence in any estimate of the underlying range size/body size relationship (Fig. 3, open circles), we show that partial samples had a higher probability of intercepting large ranging species and subsequently smaller ranging species were disproportionately under-represented in partial samples (Fig. 4, contrast solid circles and squares). Both of these biases manipulated the underlying range size frequency distribution, albeit in different ways. The first bias acted to shift larger ranging species to more intermediate regions of the

distribution, whereas the latter bias acted to remove species from the lower region of the distribution altogether. When range size is paired with body size, the resulting correlation was much weaker than the 'true' correlation (Fig. 3) because the ranges of larger-bodied species were underestimated (pulling down the right-hand side of a bivariate plot), and some of the ranges of small-bodied species were missed (pushing up the left-hand side of a bivariate plot). These are precisely the points that drive any existing relationship. Therefore, the greater the sampling partiality, the greater the likelihood of capturing non-significant relationships with higher degrees of uncertainty associated with individual samples. For example, assuming that species are continuous over their geographic range and the body size/range size relationship is strong, a single study focusing on 5% of the domain of New World mammals (e.g. the scope of a small to medium-sized country) may result in a potential relationship strength ranging from a somewhat positive to a weak negative relationship (with 95% confidence). The true relationship can never be recovered. In contrast, when the underlying relationship is weak, observed relationships may range from stronger than reality through to spuriously negative (Fig. 2b, right-hand side, black squares). Although the true relationship may be recovered, with a single sub-sample (e.g. empirical study) there is no way to evaluate how close we are to the true relationship. Therefore, single studies with moderate to highly partial samples can say nothing about the underlying relationship. Failure to detect an underlying relationship because of sampling artifacts is problematic, but the danger of reporting a relationship that is opposite to that which is found in nature is increased by sampling partiality.

By compounding sampling partiality with the fact that species typically do not occur continuously over their geographic ranges (e.g. Brown *et al.*, 1996) and that the density at which species isolates occur is typically lower in larger-bodied and larger ranging species (Damuth, 1981, 1987; Brown, 1995; Brown *et al.*, 1996; Gaston *et al.*, 1997; Gaston, 2003), we illustrate a further departure of any one partial sample from the true underlying relationship. Decreasing number of isolates per range reduced the chance of sampling large ranging species (Fig. 4, contrast triangles and circles). This artifact occurred because there was a greater chance of a partial sample missing isolates that were more spread out over their range. Rather than just truncating large range sizes, as is the case with sampling partiality, the decreased sampling likelihood of larger ranging species disproportionately removed larger ranging species from the analysis in a similar fashion to that in which sampling partiality removed smaller ranging species. The loss of the larger ranging species from the analysis – rather than just the truncation of their ranges – further reduced the likelihood of capturing any underlying relationship to the point where any random sub-sampling resulted in correlation strengths ranging from negative to positive with a mean of approximately zero (no relationship). For example, at low numbers of isolates, 5% sampling partiality results in an approximately equal chance of capturing a strong positive and strong negative correlation regardless of the strength of the underlying relationship (Fig. 2a,b, left-hand side, black squares).

The problems incurred by sampling artifacts on the range size/body size relationship can be used to our advantage by providing insight into the distribution of species over their ranges when both comprehensive and partial studies exist for a particular group. For example, as suggested by Gaston and Blackburn (1996) and quantitatively supported here, if a comprehensive relationship is positive, but the partial is negative, then large-bodied species likely have large geographic ranges but are more patchily distributed within their ranges (i.e. decreased number of isolates) than small-bodied species (left-hand region of Fig. 2a). However, in contrast to their predictions, no conclusions can be made about isolate

patchiness when comprehensive and partial analyses are both positive (Fig. 2a). Note that partial analyses may be positive regardless of the number of isolates. Furthermore, the requirement for comprehensive analyses in the above examples exemplifies the current study's primary conclusion: non-comprehensive biogeographical data should not be interpreted at comprehensive scales without reference to the probability of capturing the true underlying relationship. This probability cannot be determined with reference to only one or a few partial samples.

CONCLUSIONS

The synergy of the two sampling artifacts, sampling partiality and number of isolates per range, illustrates four interesting points. First, the reduction in ability to capture the underlying range size/body size relationship was not only caused by disproportionately truncating the ranges of large ranging species and a simple decrease in sample size, but also by a non-random loss of species from the range size frequency distribution. Second, sampling artifacts influenced the median observed relationship strength more when the underlying relationship was stronger, tending to pull any correlation index towards non-significance. Third, the uncertainty caused by any combination of the sampling artifacts was similar regardless of the real underlying relationship because they affect range size independently of body size. Finally, the influence of the number of isolates on the range size/body size relationship was minimal until numbers were approximately 10–100 isolates per range. Therefore, the importance of the number of isolates as a sampling artifact will depend strongly on the geographical scale of the study and the inherent ecological properties of the study group, namely how species are distributed over their geographic range.

   In searching for general theories to describe large-scale patterns of animal and plant distributions and abundances, care must be taken to fully understand the influence of sampling artifacts before conclusions are drawn. In the context of the often-hypothesized positive relationship between range size and body size, we show here that spurious non-significant or negative relationships can easily result from such artifacts, potentially leading to conflicting conclusions (*sensu* Gaston and Blackburn, 1996). Our purpose in the present study was not to argue that the range size/body size relationship is positive, but rather to question the validity of results that are potentially driven by sampling partiality and the likelihood of finding a given species within its geographic range.

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