between molecular and morphological homology; characters are homologous when they share a common ancestry.

Grehan and Schwartz, in contrast, seem to apply different rules for molecular and morphological characters. They find convergent evolution in the coding regions of DNA to be both probable and highly problematic (Grehan & Schwartz, 2011, p. 2402): '… *not only are molecular comparisons limited to minuscule portions of genomes, most are still confined to the coding region… that codes for metabolically active proteins and enzymes, which… reflect adaptation to environmental circumstances… Similarly, because mitochondria serve only metabolic function…, demonstration of similarity between taxa in mtDNA sequence is also not necessarily a reflection of phylogenetic propinquity*'. In their earlier study, convergent evolution in morphological traits was not considered a problem (Grehan & Schwartz, 2009, p. 1826): '… *some primate biologists and systematists object to using characters with a presumed functional role because they may be the result of selection independent of phylogeny. In the absence of empirical evidence, this objection is rhetorical. We take the view that such assumptions are not relevant to phylogenetic analysis… and that the most highly corroborated hierarchically nested set of derived characters yields the most probable phylogenetic relationship…*' We see no reason why evolutionary adaptation sometimes does and sometimes does not invalidate phylogenetic inferences. Similarly, it seems inconsistent to find it a problem that only a small part of the genome can be compared among taxa, when the situation is exactly the same with morphological data.

The criticism that Grehan & Schwartz (2011) targeted against direct optimization (DO; Wheeler, 1996) seems to indicate that they mistake it for a phenetic method, although it is fundamentally cladistic and hence based on inferences about common ancestry (i.e. homology) of characters. In the classical two-step approach, 'primary' homologies are first hard-coded in the data matrix, and then 'secondary' ('true') homologies are identified during analysis. The first step (character analysis) depends on assumed phylogenetic relationships, and the results of the second step (congruence analysis, or tree search) depend on those assumptions, which compromises the validity of the congruence test (De Laet, 2005). The purpose of DO is to avoid the subjective element inherent in the two-step process by comparing all possible scenarios of homology, rather than choosing one *a priori*. The result of DO is hence based on the globally most parsimonious combination of homologies and tree topology.

Grehan & Schwartz (2011) further criticize previous studies for having polarized the character states incorrectly, and imply that they themselves have identified the correct polarization. Given that this detective story has no last page that reveals the absolute truth, arguments on who is right and who is wrong could be continued forever. We are not interested in doing so, however.

It appears that humans are highly autapomorphic in comparison to other great apes: out of all the characters Grehan & Schwartz (2011) excluded as autapomorphic, 50 were autapomorphies of humans, 5 of orangutans, 2 of chimpanzees, and 7 of gorillas. It is, therefore, possible that the human–orangutan relationship in their analysis was an artefact caused by long-branch attraction (Bergsten, 2005) – humans and orangutans simply represent the morphologically most distinct great apes. To avoid long-branch attraction, one should obtain data that breaks the long branches, such as fossil data or DNA evidence (the latter because human DNA is not as highly autapomorphic as human morphology is).

One approach to evaluating the credibility of phylogenetic hypotheses is by comparing them to external criteria. For example, Grehan & Schwartz (2009) demonstrated that the human–orangutan hypothesis provides a more parsimonious biogeographical scenario than the human–chimpanzee hypothesis, and argued that this provides external support for their phylogeny. We would like to continue in the same vein and ask about the evolutionary scenarios involved. Firstly, if the high similarity between human and chimpanzee DNA is not due to common ancestry, what kind of selection pressures could have caused a sufficient degree of convergent genetic evolution to erase the 'true' phylogenetic signal from the molecular data? Secondly, if such strong and directional selection was indeed operating on the genome, why did it not cause convergence in morphology as well? As we are unable to imagine convincing answers to these questions, we find that this particular external criterion supports the human–chimpanzee relationship rather than the human–orangutan relationship.

Samuli Lehtonen*, Hanna Tuomisto, Ilari E. Sääksjärvi and Kalle Ruokolainen

Section of Biodiversity and Environmental Research, Department of Biology, University of Turku, FI-20014 Turku, Finland
*E-mail: samuli.lehtonen@utu.fi

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Across-taxa incongruence in patterns of collecting bias

ABSTRACT

If biological collections tend to be taken near accessible areas, and the number of such areas is limited, then we should ex-

pect a similar spatial distribution of collecting effort across taxa. Alternatively, if researchers working on a given taxon pick collection localities based on idiosyncratic criteria, then there should be no spatial similarity in collecting effort. This study compares the spatial distribution of collecting effort for plants and birds in Amazonia. Collection localities were transformed into a Thiessen network where polygon size works as a surrogate for collecting effort. A correlation between botanical and ornithological datasets, with an adjustment for spatial autocorrelation, showed little congruence in the spatial distribution of collecting effort between the two taxa. This incongruence of the distribution of collection effort among taxa suggests that the identification of priority areas for research, and correction for Wallacean and Linnean shortfalls based on taxon-specific studies, should not be generalized.

INTRODUCTION

Schulman *et al.* (2007a) analysed the distribution pattern of the botanical collecting effort in Amazonia: they gathered collecting localities from herbarium collections and drew a map of Thiessen polygons, using collecting localities as polygon anchors, to visualize collecting density in a scale-independent way. The study confirmed that botanical collecting activity in Amazonia still has a severe spatial bias, with uncollected areas representing 43% of the basin's area. These spatial knowledge gaps have important consequences for perceived patterns of species richness and conservation prioritization. Successful conservation of biodiversity depends, in part, upon an accurate assessment of the diversity to be preserved (Winker, 1996).

Studies in tropical forests around the world have demonstrated that there is a strong bias in the distribution of collecting effort, which inflates species richness around the sampled areas (Nelson *et al.*, 1990; Kress *et al.*, 1998; Peterson *et al.*, 1998; Parnell *et al.*, 2003; Reddy & Dávalos, 2003; Schulman *et al.*, 2007a; Tobler *et al.*, 2007; Vale, 2011; Werneck *et al.*, 2011). Indeed, this

effect is strongly evident across Brazil, the country with the most tropical forest, where predictions of the regional plant species remaining undiscovered ranged from 9% to 49% due to geographical differences in research effort (Pimm *et al.*, 2010). The consequence of well-collected areas appearing to have the highest species concentrations is that they are often identified as top conservation priorities for their alleged unusually high biodiversity (e.g. Reddy & Dávalos, 2003; Schulman *et al.*, 2007b; Vale, 2011). Once these areas are singled out, poorly documented areas that might be of equal or greater importance may be ignored (Bates & Demos, 2001). This potential bias is especially worrisome in the tropics, which combine high biodiversity with low levels of biological collection and rapid habitat loss (Prance *et al.*, 2000).

At a regional scale, knowledge gaps might be spatially congruent among taxa. If that is the case, then one could use studies for one taxon to correct these gaps for the so-called Wallacean and Linnean shortfalls across taxa (Whittaker *et al.*, 2005; Bini *et al.*, 2006; Schulman *et al.*, 2007a). Because biological collections tend to be made in or near accessible areas (Peterson *et al.*, 1998; Parnell *et al.*, 2003; Reddy & Dávalos, 2003; Tobler *et al.*, 2007), and there are a limited number of such areas in Amazonia, we should expect a similar spatial distribution of collecting effort across taxa. Alternatively, researchers working on a given taxa might pick collection localities based not only on accessibility but also on a set of idiosyncratic criteria. If that is the case, then the spatial distribution of collecting effort should not be similar across taxa. Therefore, any attempt to correct for sampling bias based on a single taxon should not be generalized.

Here we compare the plant dataset used by Schulman *et al.* (2007a) with a dataset on ornithological records to assess whether the spatial distribution of collecting effort is similar across taxa in Amazonia.

MATERIALS AND METHODS

We obtained ornithological collection localities from the ornithological gazetteers of the Neotropics (Paynter, 1982, 1988, 1989, 1992, 1993, 1994, 1995, 1997; Stephens & Traylor, 1983, 1985; Paynter & Traylor, 1991; Vanzolini, 1992). These gazetteers provide geographical coordinates for ornithological collection localities, compiled from the literature and museum collections. The gazetteers do not provide a

list of species recorded at the locality or a measure of collecting effort at the locality. From one perspective, the ornithological gazetteers could overestimate effort by including localities where no inventory actually occurred, such as mere camping sites (da Silva, 1995). From another perspective, gazetteers could underestimate effort by having only one record for a locality where many separate collections might have occurred. The printed gazetteer records were individually entered into a digital database and then cleared of any ill-defined localities (e.g. entire rivers, states or parks). A total of 1328 unique ornithological collecting localities were within Amazonia (as defined by the digital ecoregion database, Olson *et al.*, 2001).

Schulman *et al.* (2007a) used the herbarium databases of the New York Botanical Garden (NYBG), queried in 2002, and the VAST nomenclatural database of the Missouri Botanical Garden, queried in 2006. We used only the NYBG database in the present study, to maximize consistency with the ornithological database in terms of the number of records and time span. The NYBG dataset, provided by Leif Schulman (Botanic Garden, University of Helsinki, Finland), had 2027 unique botanical collecting localities in Amazonia. Because the ornithological dataset was smaller than the botanical dataset, we took 1000 random subsamples from the botanical dataset of the same size as the ornithological dataset (1328 localities).

Following the procedure of Schulman *et al.* (2007a), we converted the ornithological collection localities and the 1000 subsamples of the botanical collection localities into networks of Thiessen polygons. The Thiessen networks were used to evaluate the geographical congruence in collection effort between the datasets. In a Thiessen network, each polygon contains only one collection locality (anchor point). Within each polygon, any given point is closer to its collection locality than to collection localities of all other regions (Lo & Yeung, 2002). The larger the polygon, the lower the collection intensity because the area represented by a single collection locality is greater. Therefore, we can use polygon size as a surrogate for collecting effort. If ornithological and botanical networks are similar, then in any given area their constituent polygons should have similar sizes.

To sample polygon size within the Thiessen networks, we used a total of 407 sampling points with 1° spacing, covering

Amazonia. To avoid sampling Thiessen polygons that might have been artificially truncated by the boundary of Amazonia, these sampling points were placed a minimum distance of 100 km from the edge of Amazonia.

If the distribution of collecting effort was similar, then areas with small polygons (well collected) and with large polygons (poorly collected) should have coincided in the botanical and ornithological datasets. To evaluate whether there was congruence between polygon sizes in both datasets, we performed a correlation analysis between the ornithological and botanical polygon sizes using the corrected number of degrees of freedom from Dutilleul's method for spatial autocorrelation adjustment (Dutilleul, 1993) within the SAM 4.0 software (Rangel et al., 2010).

RESULTS AND DISCUSSION

Visual examination of the ornithological and botanical Thiessen networks showed some similarities (Fig. 1). In both datasets, for example, north-eastern Amazonia outside Brazil was relatively well collected while south-east Amazonia was massively under collected. The average botanical Thiessen polygon (25,219 km^2 ± 698 SE) was larger than the average ornithological Thiessen polygon (16,979 km^2 ± 413 SE). This disparity may seem counterintuitive, as the network of Thiessen polygons of each dataset was built from the same number of collecting localities. However, the larger average polygon size calculated for the botanical dataset was a consequence of very strong spatial aggregation of collecting localities in the botanical dataset and the 1° sampling necessary for this particular comparison. The effect was that clusters of small polygons were so small that they did not all contribute to the calculated average polygon size, because they were finer than the analysis scale.

Dutilleul's analysis revealed an important spatial autocorrelation within the datasets, with degrees of freedom dropping from 405 to 85.5 (± 0.20 SE) on average for the correlation between the ornithological dataset and the 1000 random subsamples of the botanical dataset. The analysis consistently showed a weak correlation between the ornithological and botanical datasets, with Spearman's r = 0.327 (± 0.001 SE), and most P-values < 0.01 (59 correlations with P < 0.001, 681 with P < 0.01, 258 with P < 0.05, and 2 not significant) (Fig. 2). Apparently, non-congruent idiosyncratic

clustering of botanical and ornithological collections overrode any general similarity in spatial patterns of collecting effort between the two datasets. Idiosyncratic clustering in the botanical dataset included, for example, intense collecting on the Brazil–

Bolivia border (Fig. 1b), which reflected the activity of one of NYBG's curators and his Brazilian collaborators (Hannah Stevens, New York Botanical Garden, Bronx, NY, USA, pers. comm.). Similarly, in the ornithological dataset there was intense collect-
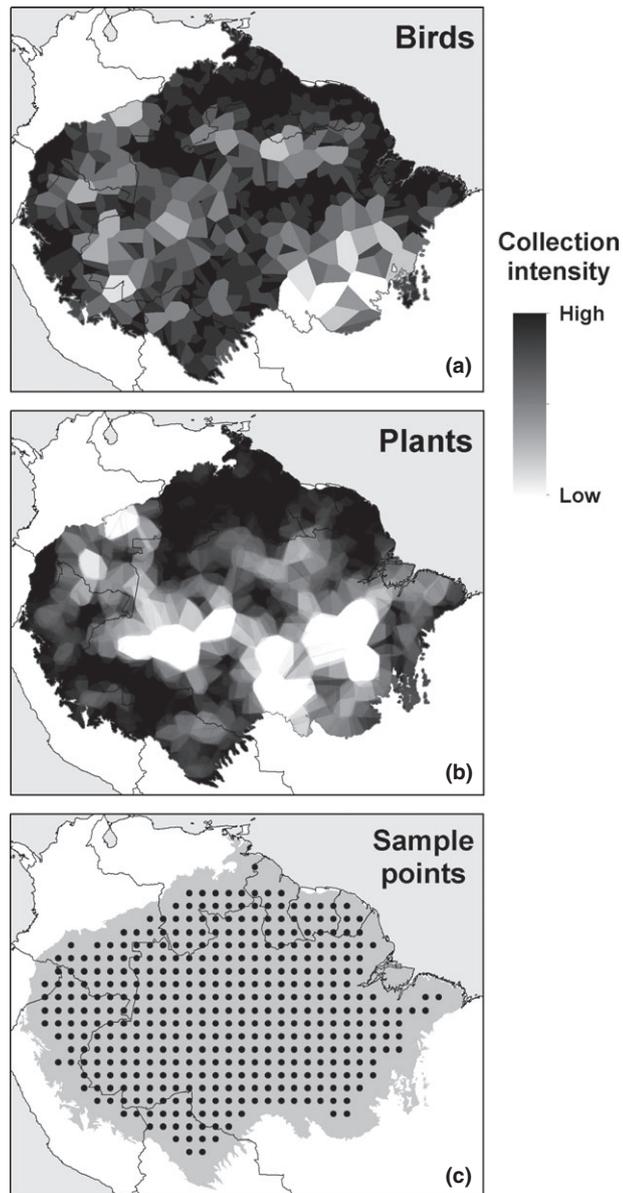

Figure 1 Summary of Thiessen polygon networks in Amazonia derived from (a) ornithological collecting localities and (b) botanical collecting localities, and (c) 407 sampling points with 1° spacing used to sample polygon size for correlation analyses. Collection intensity in (a) and (b) corresponds to the size of the Thiessen polygons, where larger polygon size (lighter grey) indicates a larger area represented by a single collection locality. For the ornithological data, the polygons shown are from the single Thiessen network (total number of collecting sites was 1328). For the botanical data, the polygons shown are an average of the 1000 Thiessen network, generated from subsets with the same size as the ornithological data (in order to calculate this average the 1000 networks were transformed into rasters with 10 km resolution).
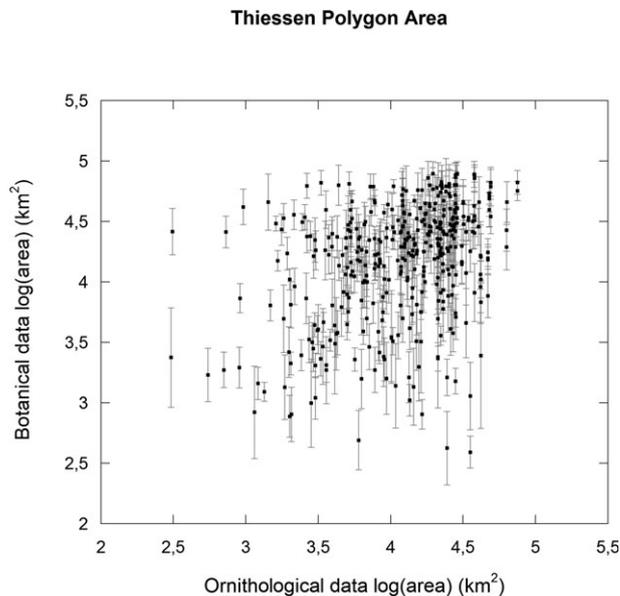
Thiessen Polygon Area

Figure 2 Linear correlation between ornithological and botanical Thiessen polygon size within Amazonia using Dutilleul's method for spatial autocorrelation adjustment (average Spearman's $r = 0.351$, corrected $P < 0.001$). Botanical data represent the average polygon size and standard deviation among 1000 subsamples. If the distribution of botanical and ornithological collecting effort is similar, there should be a positive relationship between polygon sizes.

ing along major rivers (Fig. 1a), which reflected not only accessibility but also the relevant role of large and small interfluves on the distribution of Amazonian birds (Vale *et al.*, 2008).

The practice of conservation uses information such as richness of indicator taxa, endemism, or higher taxon richness to identify possible conservation areas (van Jaarsveld *et al.*, 1998). The assumption of surrogacy involved in these area selection schemes is not widely accepted, however, because geographical areas with high richness tend to vary taxonomically (e.g. van Jaarsveld *et al.*, 1998; Andelman & William, 2000; Ceballos & Ehrlich, 2006; Grenyer *et al.*, 2006). The present study suggests that geographical areas with knowledge gaps also vary taxonomically, at least in the set of data used. Further analysis would be needed, however, to verify the generality of these results. We conclude that the identification of priority areas for research and the correction for Wallacean and Linnean shortfalls should: (1) be based on as much of the available data as possible, and (2) be either taxon-specific, or use a multi-taxonomic approach in order to achieve generality.

Mariana M. Vale[1]* and
Clinton N. Jenkins[2]

[1]*Departamento de Ecologia, Universidade Federal do Rio de Janeiro, C.P. 68020, Rio de Janeiro, RJ 21941-590, Brazil*, [2]*Department of Biology, North Carolina State University, Campus Box 7617, Raleigh, NC 27695, USA*
**E-mail:* mvale.eco@gmail.com*

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