ORIGINAL ARTICLE

Beta diversity of frogs in the forests of New Guinea, Amazonia and Europe: contrasting tropical and temperate communities

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ABSTRACT

Aim To test the hypothesis that animal communities within environmentally relatively uniform lowland forests are characterized by low beta diversity, both in tropical and in temperate areas.

Location Lowland forests in the basins of the Sepik and Ramu rivers in New Guinea, the Amazon river in Bolivia, and the Elbe and Dyje rivers in the Czech Republic.

Methods A network of 5–6 study sites spanning distances from 20–80 to 300–500 km in each study area was systematically surveyed for all frogs, using visual detection and call tracking. The community data were analysed for alpha and beta diversity.

Results Local (alpha) diversity of frog communities was similar in the two tropical areas, New Guinea (mean ± SE of 22 ± 1.4 species per site) and Amazonia (24 ± 1.7 species), but was significantly lower in Europe (8 ± 0.8 species). In Amazonia, 36 of the total of 70 species were recorded from single sites. In contrast, widespread species dominated in Europe, whereas New Guinea exhibited an intermediate pattern with both local and widespread species well represented. The rate of species accumulation across different sites was lowest in Europe, intermediate in New Guinea and highest in Amazonia. The regional species diversity, expressed as the combined number of species from five study sites, was 1.5 times higher than the local species diversity at a single site in Europe, 2.0 times higher in New Guinea and 2.7 times higher in Amazonia. The proportion of species shared between communities decreased with geographic distance in New Guinea and Europe, but not in Amazonia.

Main conclusions Frog communities in the lowland tropical rain forests of New Guinea and Amazonia had similar numbers of species, but differed in their beta diversity. More species in Amazonia had restricted distributions than in New Guinea. Both tropical areas had markedly higher alpha and beta diversity than the temperate area in Europe.

Keywords
Alpha diversity, amphibians, biodiversity, Bolivia, community similarity, geographic distribution, Melanesia, rain forest, Sepik River, species turnover.

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INTRODUCTION

A large proportion of the world's tropical forests consists of lowland rain forests situated in basins of major tropical rivers, such as the Amazon, the Congo, and the Sepik–Ramu and Fly–Strickland river systems of New Guinea. These forests also form a major part of the three remaining Tropical Wilderness Areas, defined as large pristine areas exceeding 10,000 km² of which > 70% is free from anthropogenic disturbance (Mittermeier *et al.*, 2003). It is therefore unfortunate that the distribution of biodiversity within these large blocks of forest is particularly poorly understood (Novotny *et al.*, 2007).

Apart from their importance for biodiversity conservation, lowland rain forests represent a conveniently simplified study system for the analysis of beta-diversity patterns. Large contiguous areas of lowland forest that lack obvious dispersal barriers and steep environmental gradients are expected to be rather uniform biologically, hosting communities characterized by high alpha but low beta diversity (Novotny *et al.*, 2007). This assumption is in need of empirical testing, ideally using multiple plant and animal taxa with diverse ecologies and dispersal abilities.

There is no consensus on the rate of change in species composition (i.e. beta diversity) in plant and animal communities across distances from tens to thousands of kilometres within lowland rain forests. For instance, insect beta diversity was recently estimated to be very high in lowland Amazonia (Erwin *et al.*, 2005), but fairly low in New Guinea (Novotny *et al.*, 2007; Hulcr *et al.*, 2008).

The relative importance of spatial variability in environmental conditions, the dispersal limitation of species, and inter-specific interactions as determinants of beta diversity is also poorly understood, particularly for animals. Plant studies found both dispersal limitation and variability in environmental factors, particularly climate and soil variables, to be important for plant beta diversity in Amazonia (Condit *et al.*, 2002; Tuomisto *et al.*, 2003). The turnover of plant species over long distances was low, with 1-ha plots 100 km apart sharing 40% of all tree species, whereas those 1400 km apart still shared 20% of species. However, this low turnover was still higher than that reported for plants in boreal forests (Condit *et al.*, 2002).

Beta-diversity studies of plants, and even more so of arthropods and other small animals, are impeded by poor taxonomic knowledge of tropical species, making comparisons of samples across communities difficult. However, there are very few studies exploring species turnover between even the most taxonomically well known and intensely studied vertebrate communities.

The focus of vertebrate studies has traditionally been on large-scale biogeographical patterns and the analysis of regional species pools and the geographic distribution of vertebrate species, rather than on communities (e.g. Allison, 1996; Murray *et al.*, 1998; Duellman, 1999a; Rahbek *et al.*, 2007). This analytical bias may be because of the predominantly qualitative methods used for vertebrate surveys. Botanists often count individual plants in forest plots, whereas entomologists count insects in light, Malaise, pitfall and other quantitative samples. These data are better suited to the analysis of community patterns than the simple species lists that are available for most vertebrate assemblages.

Beta-diversity studies are often designed as single, non-replicated projects, measuring beta diversity *per se*, rather than its variability in response to potential environmental drivers. This is not surprising because beta-diversity studies are logistically demanding, requiring data from multiple, geographically widely spaced communities. These problems notwithstanding, replicated studies are crucial for analyses of beta-diversity determinants.

Replicated studies of beta diversity along latitudinal gradients that contrast tropical and temperate forests, and replicated studies from different continents within the tropics that examine the community patterns arising from different regional pools of species are arguably among the most promising approaches to the study of beta-diversity determinants (Koleff *et al.*, 2003b; Primack & Corlett, 2005). Such studies are rare because biologists often use different survey protocols when working in temperate and in tropical ecosystems (Novotny & Weiblen, 2005). Furthermore, tropical biologists tend to specialize on the biota of a particular continent, making inter-continental comparisons difficult to accomplish.

The present study fills some of these gaps by providing basic exploratory data for frogs, an important vertebrate group forming species-rich communities in tropical rain forests. It includes multiple beta-diversity analyses, comparing two major tropical areas, New Guinea and Amazonia, with temperate Europe.

MATERIALS AND METHODS

Study sites and surveys

The New Guinea study was conducted at five sites within a 500×150 km area of lowland rain forest ($03°24'–05°14'$ S, $141°05'–145°12'$ E, 40–250 m a.s.l.) in the basin of the Sepik and Ramu rivers (Fig. 1). The study sites were selected so that they incorporated a similar range of forest types, climates and altitudes. The vegetation at all study sites was classified as mixed evergreen hill forest (Paijmans, 1976), and the climate humid with a mean annual rainfall of 2000–4000 mm and a mean monthly air temperature of 26°C (McAlpine *et al.*, 1983).

Each study site was surveyed once during the rainy season between May 2004 and March 2005. All suitable habitats, including primary and secondary forest vegetation, swamps, streams and stagnant pools, were searched within an area of *c.* 5 km^2 at each site. The surveys were conducted for 13–20 consecutive days and nights per site. The night surveys took place typically between 18.30 and 03.30 h. Frogs were detected visually using a headlamp and by calls, which were recorded with a Sony TCM 5000 tape recorder and a Sennheiser ME66 microphone. Frog specimens were photographed alive, and voucher specimens of each species were retained for identification of difficult taxa. These are deposited at the University of Papua New Guinea (Port Moresby) and the South Australian Museum (Adelaide). Body size (snout–vent length) was determined for each species to the nearest 0.1 mm, and each species was classified as a terrestrial or aquatic breeder depending on whether they require water for larval development. In New Guinea, a large proportion of species, including all Microhylidae and Ceratobatrachidae, undergo direct embryonic egg development independent of water (Zweifel & Tyler, 1982). New Guinea sites were surveyed by C.D. and frogs were identified by S. J. R. and C.D. Further details are reported in Richards (2007) and Austin *et al.* (2008).
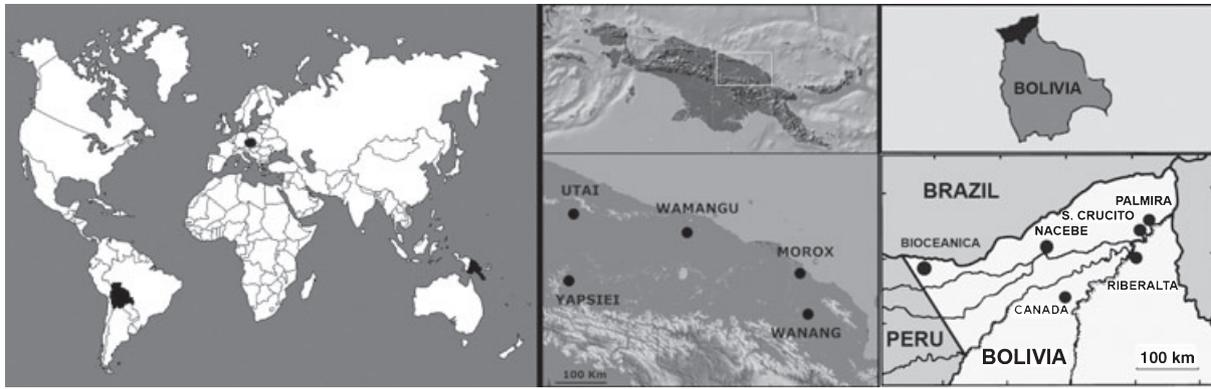
Figure 1 Map of the three study areas (left), and the study sites in New Guinea (centre) and Bolivia (right).

The Amazonia study included six sites within an area of lowland rain forest *c.* 400 × 120 km (10°35′–11°45′ S, 65°44′–69°22′ W, 160–300 m a.s.l.) in Bolivia (Fig. 1). All study sites were humid, with a long wet season, 1800–2200 mm of annual rainfall and a mean annual temperature of 27–29°C (de la Riva *et al.*, 2000). The surveyed areas included the following habitats: (1) more or less disturbed primary 'terra firme' forest, (2) plots of seasonally flooded forest, (3) forest swamps and lagoon, brook and river shores, (4) forest margins and various types of secondary growths, and (5) forest fields, plantations and pastures. Each study site was surveyed once during the season of heavy rains between November 1999 and November 2007. The surveys were conducted for 9–16 person-days and nights per site, using the same protocols as in New Guinea. Amazonian frogs were surveyed and identified by J.M. Further details of the samples are reported in Moravec & Aparicio (2000, 2004a,b, 2005, 2006).

The European study included six sites within a 280 × 220 km area located in lowland regions along the Czech and Moravian rivers Ohre, Ploucnice, Elbe, Dyje and Morava (48°43′–50°41′ N, 13°16′–16°58′ E, 150–450 m a.s.l.). The sites comprised a mosaic of open and forested habitats, generally with considerable anthropogenic modification. Further details of the samples are reported in Honcu & Vitacek (1990), Sebela (1992), Reiter & Hanak (2000), Vozenilek (2000) and in unpublished data by J.M.

The detectability of frogs was probably highest in Europe owing to the concentration of breeding populations around water bodies. A large proportion of Amazonian and New Guinean frogs have reproductive strategies independent of free-standing water, so populations are more dispersed during breeding. To minimize this potential bias, our surveys targeted calling frogs throughout each site on each continent. Given our search effort at each site, the detectability of vocalizations by frogs in Europe, Amazonia and New Guinea is unlikely to be significantly different.

Although a number of studies have revealed cryptic diversity in some widespread tropical frogs (e.g. Wynn & Heyer, 2001; Elmer *et al.*, 2007; Fouquet *et al.*, 2007), our survey technique combined careful assessment of the acoustic parameters of nearly all frog species with examination of morphological characters to support taxonomic conclusions. Given the importance of call as a species recognition system in frogs (Lougheed *et al.*, 2006), we are confident that few if any unrecognized cryptic taxa are included in this study. Our lists of species for each site include undescribed taxa identified by us as cryptic species during this study on the basis of calls and genetic data.

Data analysis

Differences in species composition between sites were quantified by the Jaccard similarity index; that is, by the proportion of shared species from the combined total of species found at the two compared sites (Koleff *et al.*, 2003a). The correlation between Jaccard similarity and geographic distance was tested with the Mantel test using all possible pairs of study sites.

The completeness of each survey was assessed by constructing species accumulation curves that show the rate of new species discovery during the survey. The rate of increase in total species richness with increasing number of surveyed sites in each of the three regions was assessed from species accumulation curves that combined sites in random order. All possible subsets of sites from the total of 5–6 sites studied in each area were used to estimate the mean, minimum and maximum species richness for each particular number of sites. The total number of species expected in each studied area was estimated using the Chao 2 index, suitable for the analysis of species lists from multiple sites (Colwell & Coddington, 1994).

The geographic distribution of each species was characterized by the number of sites at which it was recorded and by the maximum geographic distance between the occupied sites. Pair-wise distances between our study sites ranged from 80 to 503 (median 290) km for New Guinea, from 20 to 400 (170) km for Amazonia, and from 20 to 330 (220) km for Europe. We therefore used the distance of 250 km, close to the median distances between sites in our three study areas, to separate species with restricted and widespread distribution. The widespread species were defined as those found at sites > 250 km apart, restricted species as those at multiple sites < 250 km apart, and local species as those at a single site. The

geographic distribution analysed here is not a substitute for the size of the species' geographic range, but is a different characteristic of distribution, measuring the frequency of occurrence within the species' geographic range.

RESULTS

We recorded 44 species of frogs at the New Guinean sites, 70 species at the Amazonian ones and 12 species at the European ones, representing 14 families (Fig. 2, Tables S1–S3). All New Guinean sites were dominated by members of the family Microhylidae, and all Amazonian sites by members of the family Hylidae (Appendix S1). The proportion of species represented by the most species-rich family did not vary among sites within each study area (chi-square test, $P > 0.05$; other families could not be tested as they had too few species).

Local species diversity was well sampled, as indicated by the fact that species accumulation curves approached an asymptote or only gradually accrued species for all but three of the 11 tropical study sites (Fig. 3) as well as for all the European sites (not shown). Local species diversity ranged from 20 to 27 species (mean 22 species) at the New Guinean sites, from 16 to 28 (mean 24) species at the Amazonian sites and from 6 to 11 (mean 8) species at the European sites. The local (alpha) diversity was not significantly different between the two tropical study areas, but was significantly lower in Europe (ANOVA with Tukey's *post hoc* tests, $P < 0.01$).

Frog communities in Europe, and to a lesser extent in New Guinea, were dominated by widespread species, whereas species with intermediate geographic ranges (found at multiple sites < 250 km apart) and species sampled at single sites constituted only a minority component in each community. The Amazonian communities showed a distinctly different pattern, with species sampled at single sites and species with an intermediate distribution more prominent (Fig. 4a).

The number of species restricted to single sites accumulated rapidly when increasing numbers of sites were combined. This was particularly the case for Amazonia, where 36 of the total of 70 species were recorded from single sites. In contrast, the combined list of European species remained dominated by widespread species. New Guinea exhibited an intermediate pattern, as both species sampled from single sites and widespread species were well represented (Fig. 4b).

Body size and mode of reproduction (terrestrial vs. aquatic) were not significant explanatory variables for the geographic distribution of New Guinean species, expressed as the longest distance between sites at which the species occurred ($P > 0.05$, general linear model with reproduction as a categorical variable).

Differences in the geographic distribution of species among the study areas translated into different slopes of species accumulation curves (Fig. 5a). In particular, the combined number of species from five study sites was only 1.5 times higher than the mean number of species at a single site in Europe, 2.0 times higher in New Guinea and 2.7 times higher in Amazonia. The number of species estimated for the whole area by the Chao 2 (± SD) index was 64 ± 13 species for New Guinea, 123 ± 25 species for Amazonia and 12 ± 0.2 species for Europe. Our sampling thus underestimated the regional species richness in the tropics, particularly in Amazonia, but not in Europe. The estimates of species richness for large geographic areas based on data from a limited number of sites are inevitably unreliable, but can still be used as a means of comparing richness per unit of sampling effort (O'Dea *et al.*, 2006), pointing here to higher richness in Amazonia than in New Guinea.

The number of frog species found only at single sites increased with increasing number of surveyed sites in Amazonia, but decreased in New Guinea and Europe (Fig. 5b). The sampling of additional sites adds new species from these sites to the overall data, but also leads to the discovery of additional sites for species previously considered restricted to a single site. The balance of these processes determines the overall trend in the number of locally endemic species with increasing number of sampled sites.

The proportion of species shared between communities (Jaccard similarity) decreased with geographic distance between the communities in New Guinea and Europe, but not in Amazonia (Fig. 6). The Amazonian communities were characterized by generally low similarity values (mean 0.23),
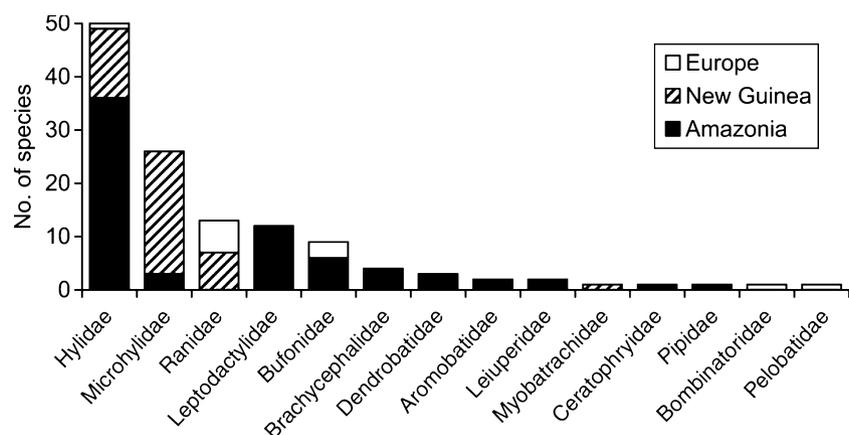

Figure 2 Family composition of lowland frog communities in New Guinea, Amazonia and Europe. The total number of species from each family recorded from all study sites within each study area is shown. No species occurred in more than one area.
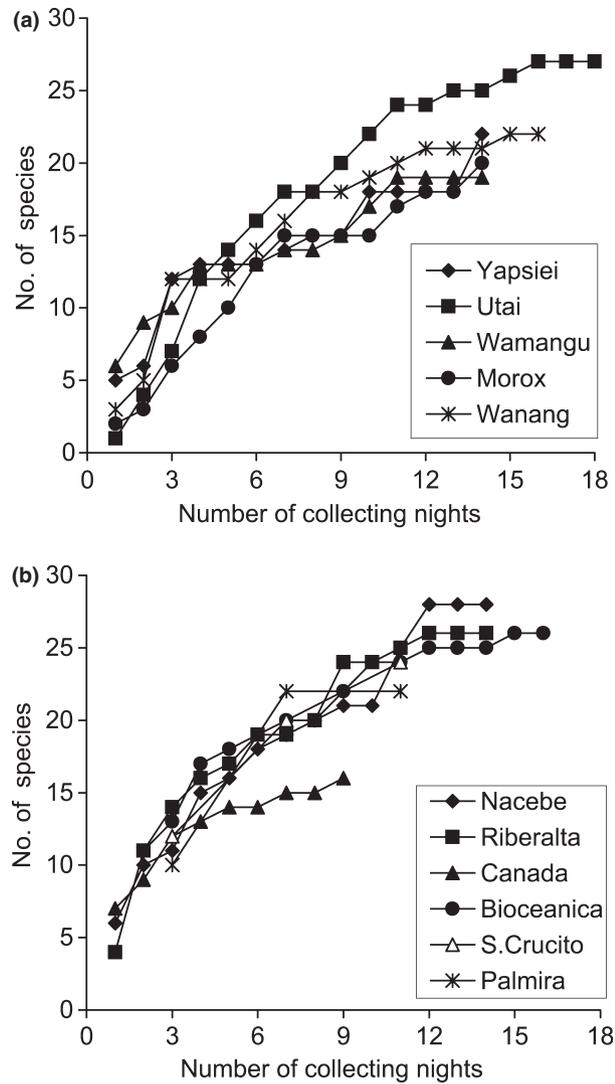
(a)

(b)

Figure 3 Species accumulation curves for individual study sites in (a) New Guinea and (b) Amazonia. Cumulative totals for the number of frog species recorded at each study site obtained by amalgamating individual survey nights from the start to the finish of each survey are shown.

(a)

(b)

Figure 4 Geographic distribution of frog species in individual communities (a) and combined data from all sites (b) in New Guinea, Amazonia and Europe. Mean (SE) numbers of species found at a single site, multiple sites spanning < 250 km, and multiple sites spanning > 250 km (shown in a) are significantly different between Amazonia and the two other areas (ANOVA with Tukey's comparisons, $P < 0.05$). The regional lists of species (shown in b) differ in geographic distribution between Amazonia and Europe (ANOVA on ranks with Dunn's comparisons, $P < 0.05$). See Materials and Methods for details of geographic distribution categories.

independent of their geographic distance. In contrast, New Guinean communities had higher similarity values (mean 0.40), falling from 0.70 for the closest to 0.28 for the most distant pairs of sites. The European communities exhibited the highest overall similarity values (mean 0.58), but these values were also correlated with geographic distance.

DISCUSSION

The local species richness at our New Guinean sites was within the range expected for lowland rain forests. Other studies reported 12–30 frog species from similar habitats in New Guinea (Allison *et al.*, 1998; Read, 1998; Richards, 2002). In contrast, the species diversity at our Amazonian sites was relatively low compared with the 29–81 species (average 48
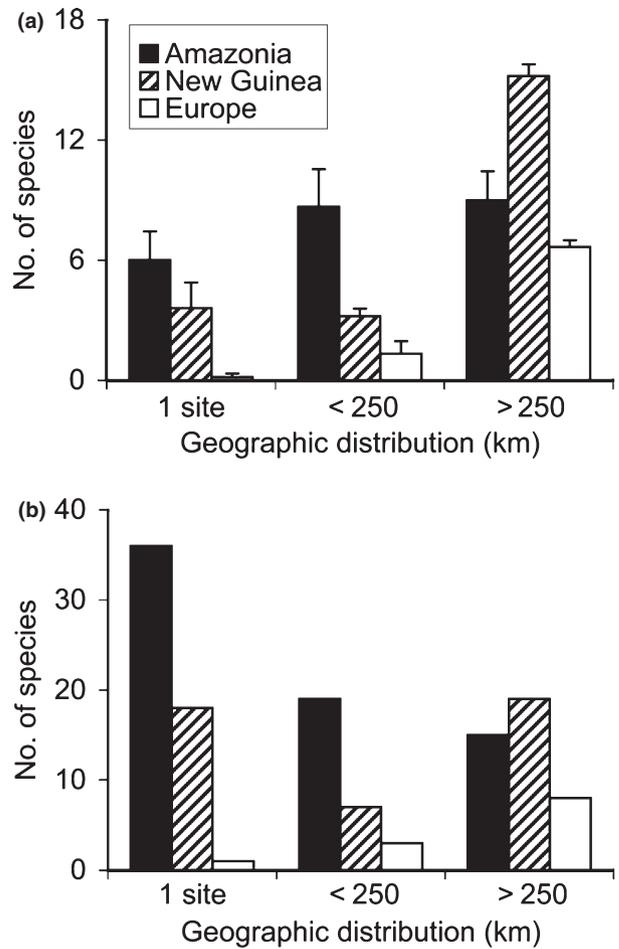
species) reported from 18 other sites (Duellman, 1997, 1999b, 2005). However, most of these other sites were visited repeatedly and for longer periods of time than were our study sites. The thoroughness of the survey and the size of surveyed areas, considered as individual study sites, are the main variables complicating the analysis of the numbers of species at different sites in the Amazon basin (Duellman, 2005). However, our Bolivian data provide adequate comparison with New Guinea, as in both study areas the surveys were of similar duration, used the same methods and targetted areas of similar size.

The dominance of Hylidae is universal throughout Amazonian rain forest communities (Duellman, 1988), as is the dominance of Microhylidae in New Guinean lowlands (Richards, 2002). There has been a major radiation for this family in
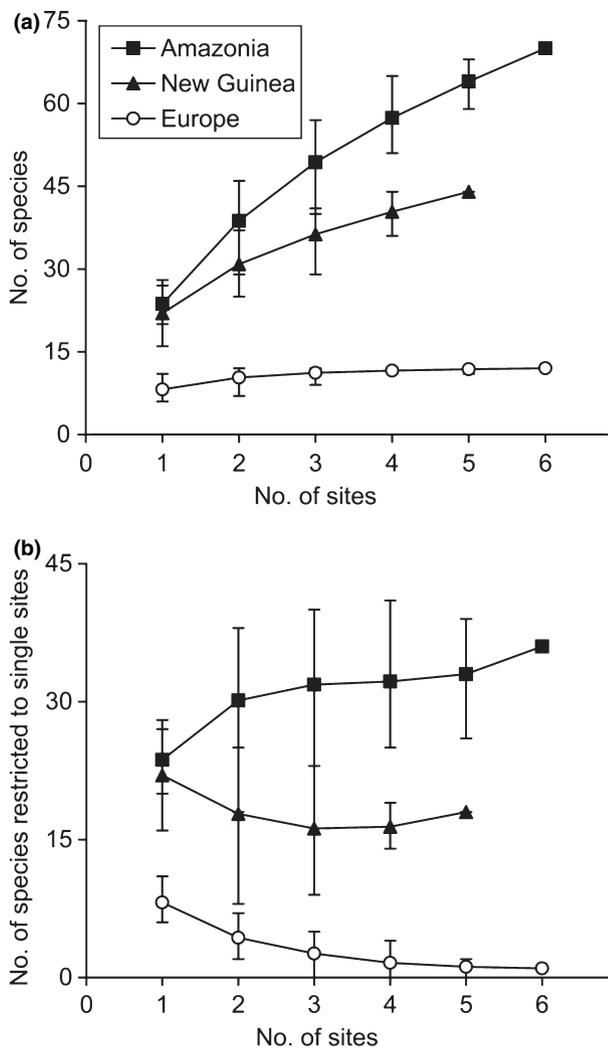
Figure 5 The number of (a) all frog species and (b) frog species known only from single sites in the composite sample in New Guinea, Amazonia and Europe. All possible subsets of the five New Guinean, six Amazonian and six European sites were used for each particular number of sites. Mean (markers), minimum and maximum (bars) values are reported for the replicated subsets.

New Guinea (Pough *et al.*, 2004). Several lines of evidence point to a higher beta diversity and more restricted geographic distributions of Amazonian frogs compared with New Guinean species. Amazonian communities have a higher proportion of species known only from single sites, and the number of these species increases with increasing geographic coverage of sampling. The species accumulation across sites is thus relatively rapid, and the regional diversity, both sampled and estimated, is high in comparison to New Guinea. The distribution of Amazonian species is highly patchy, so that even nearby sites have highly dissimilar communities. For instance, Amazonian sites < 100 km apart are less similar to one another than are New Guinean communities 500 km apart. The regional diversity of amphibians, quantified as the number of species in quadrats of *c.* 3000 km^2, is markedly
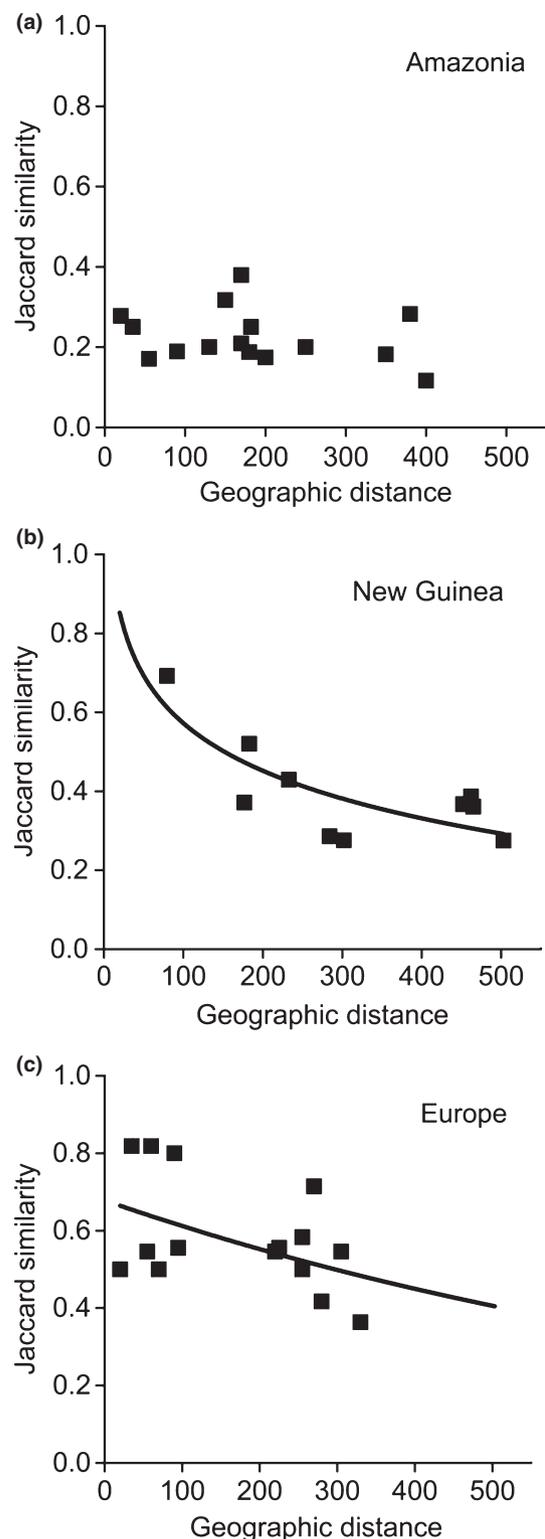

Figure 6 Similarity decay in frog communities with geographic distance. Jaccard similarity is shown for all pair-wise comparisons between study sites in Amazonia, New Guinea and Europe. The community similarity decreased with distance only in New Guinea and Europe ($P < 0.05$, Mantel test). The data were best fitted by a logarithmic function in New Guinea: Similarity = −0.1738 ln (Distance) + 1.3727 ($R^2 = 0.63$), and by an exponential function in Europe: Similarity = 0.678 e$^{-0.001\text{Distance}}$ ($R^2 = 0.23$).

higher in Amazonian than in New Guinean lowlands (Buckley & Jetz, 2007). Our study suggests that this difference is driven largely by differences in beta diversity between the two areas.

The interpretation of similarity patterns between communities is difficult without additional data on the biology of frog species and environmental variables from the studied sites. The effect of distance *per se*, particularly in the context of frog dispersal, is often compounded by changing environmental conditions with distance (Steinitz *et al.*, 2006). Rainfall patterns (Duellman, 2005) and habitat fragmentation (Cushman, 2006) are generally important determinants of frog distribution, but their effect was probably limited at our study sites because all sites were characterized by high annual rainfall. Body size is correlated with geographic range size in frogs (Murray *et al.*, 1998), but we failed to detect any correlation between body size and distribution among different sites in our New Guinea data.

We have documented lower alpha and beta diversity of temperate than of tropical communities. Temperate communities tend to have generally lower beta diversity than tropical ones, although this trend is not as uniform as that for alpha diversity (Koleff *et al.*, 2003b; Soininen *et al.*, 2007).

Both New Guinea (Allison, 1996) and Bolivian Amazonia (Köhler & Lötters,1999; Moravec & Aparicio, 2004a,b) harbour a rich herpetofauna. The Papua New Guinean fauna includes 278 and the Bolivian one 268 described species (Frost, 2007), as well as many unknown species. For example, on average > 10 new frog species are described annually from New Guinea (Günther, 2006). The present survey also produced previously unknown species (Moravec *et al.*, 2006; Richards, 2007). Our samples of respectively 44 and 70 species from the New Guinean and Bolivian study areas represent only a small fraction of the regional species diversity. In contrast, the European samples contain a total of 12 species out of the 15 species known from Central Europe (defined as including the Czech Republic, Germany, Slovakia, Hungary and Austria, and thus approximately the size of Bolivia), representing 80% of the regional diversity.

The present study applied quantitative community analysis, routinely used in the study of plant or insect communities, to obtain one of the few quantitative estimates of beta diversity in amphibian communities. This approach confirmed well-established trends of increasing alpha and beta diversity from temperate to tropical communities, but also revealed rather unexpected differences in beta diversity between tropical amphibian communities from New Guinea and those from Amazonia. We suggest quantitative community analysis as a promising approach with the potential to reveal interesting patterns of species distribution, particularly if applied to the wealth of data already available on amphibian communities.

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SUPPORTING INFORMATION

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

Appendix S1 Species illustrating the frog families at our study sites.
Table S1 Frog species recorded from the New Guinean sites.
Table S2 Frog species recorded from the Amazonian sites.
Table S3 Frog species recorded from the European sites.

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