Mesoscale spatial ecology of a tropical snake assemblage: the width of riparian corridors in central Amazonia

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Large-scale biogeographical determinants of snake assemblages may underestimate the effects of local factors that operate within restricted areas. We determined the influence of ecological gradients on the richness and species composition of snakes in the Reserva Ducke, Manaus, Amazonas, Brazil. Multivariate analyses revealed aspects of habitat selection by snakes which would be impossible to detect with large-scale approaches. There was no evidence for a relationship between the number of species recorded per plot and any of the variables measured. However, the species composition, based on a matrix of Chao dissimilarities between plots, differed significantly between riparian and non-riparian areas. The results have important implications for management and conservation, because Brazilian environmental legislation only provides protection up to 30 m away from streams like those of Reserva Ducke, while snakes use larger riparian areas. If only the areas contemplated by law are protected, the majority of species associated with riparian areas are at risk.

Key words: community structure, ecological gradients, riparian zones, tropical rainforest

INTRODUCTION

Snakes are mobile organisms. Some species undertake regular migrations between foraging and denning sites (Dixon & Soini, 1975; Duellman, 1978; Martins & Oliveira, 1998), whereas non-migratory species cover large areas within their home ranges (Shine, 1977), and long-term surveys of a single site therefore generally result in good estimates of the species richness and composition of a region (Strüssmann & Sazima, 1993, Martins & Oliveira, 1998; Bernarde & Abe, 2006; França & Araújo, 2007). If habitats are considered discrete and habitat use is registered on a presence–absence scale, most species are found to occupy a wide range of habitats, but this may mask patterns of specificity in resource use (Luiselli, 2006; Luiselli & Filippi, 2006). Understanding local relationships between species and habitats is important for reserve design. Within restricted geographic areas, many organisms do not use all habitats equally, but are concentrated in specific areas along ecological gradients (trees: Gentry, 1988; understorey herbs: Tuomisto et al., 1995; Costa et al., 2005; Kinupp & Magnusson, 2005; amphibians: Rodrigues, 2006; Menin et al., 2007; Keller et al., 2009).

It is generally recognized that riparian zones are distinct from surrounding areas, even within broad-scale habitat classifications such as "ecoregions" and "terra firme" forest. This applies to many organisms that are not directly dependent on water bodies for part of their life cycle. Riparian forests provide optimal habitats for resident species (Brode & Bury, 1984) and corridors for dispersal of visitors (Naiman et al., 2005). However, the distinctness of riparian zones is controversial for some groups (Sabo et al., 2005), as different taxa use riparian zones of different widths (Drucker et al., 2008; Marczak et al., 2010). This may be a problem for conservation, because most management agencies define general riparian buffers independent of the taxa that use them (Marczak et al., 2010).

In the present study we quantified the distribution of snake species along continuous ecological gradients and between riparian and upland areas in a tropical forest in central Amazonia. By studying many species simultaneously we were able to show patterns of occurrence that could not have been detected with confidence on the basis of individual species. The results show that this tropical snake assemblage is structured in relation to local environmental gradients, and that many species use riparian zones that are much wider than those protected by Brazilian environmental legislation.

MATERIALS AND METHODS

Study site

Reserva Ducke, administered by the Instituto Nacional de Pesquisas da Amazônia (INPA), is located in the northern suburbs of the city of Manaus, Amazonas State, Brazil (coordinates of headquarters 59º52'40" – 59º52'00"W, 03º00'00" – 03º08'00"S), and has a total area of 100 km^2. Until the 1970s, the reserve was used for experiments in forestry, with cultivation of economically important plants in about 2% of the reserve. It was subsequently declared a biological reserve, and vegetation cover was kept intact (Ribeiro et al., 1999).

Reserva Ducke is predominantly covered by tropical rainforest that is not subject to flooding for long periods. Ribeiro et al. (1999) recognized three types of plant associations in Reserva Ducke associated with topographic and soil characteristics: plateau forest, slope forest and riparian forest. The predominant soil on the plateaux is a loamy, well drained and low-nutrient yellow latosol. Forest on plateaux is 35 to 40 m high, with emergent trees up

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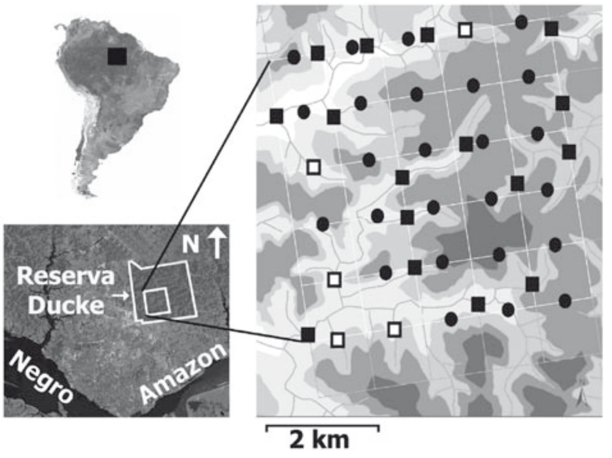

Fig. 1. Reserva Ducke, near the junction of the Negro and Amazon Rivers, with the position of the 25 km² standard PPBio grid shown by the white square. The circles represent upland uniformly distributed plots, black squares are riparian plots and open squares are uniformly distributed plots in the riparian zone. Adapted from Ribeiro et al. (1999) and http://ppbio.inpa.gov.bv, accessed 7 February 2008.

to 45 m; the understorey is dominated by sessile palms. Riparian forests are found on floodplains along streams, and have sandy soil that is waterlogged in the rainy season. Riparian forests have many plants with adventitious roots and buttresses, and the canopy is 20 to 35 m high, with few emergent trees. The understorey is dense, and composed of palms and herbs characteristic of wet areas, such as Rapateaceae, Marantaceae and Cyclanthaceae. Slope forests are transition formations between plateaux and riparian forests. Riparian areas are generally in the lower parts of the reserve, and this permits the broad classifications used by Ribeiro et al. (1999). However, the width of the riparian zone is not the same for all species, and can extend more than 100 m from the streams (Drucker et al., 2008).

The average annual temperature fluctuation is less than 5 °C, and rainfall is more intense in the period from November to April, resulting in annual averages between 1500 and 2500 mm (Alencar et al., 1979; Ribeiro & Adis, 1984).

Sample design

A 25 km² system of trails (Fig. 1) was established in Reserva Ducke in 2000 as part of the Programa de Pesquisas em Biodiversidade (PPBio) for standardized sampling and integrated surveys for long-term ecological projects (Magnusson et al., 2005). Thirty sampling plots were uniformly distributed across the 25 km² grid. Each plot was 250 m long and 5 m wide, and followed an altitudinal contour (Magnusson et al., 2005). This design keeps habitat characteristics such as soil type, depth to the water table and vegetation structure relatively uniform within each plot. However, only five of the uniformly distributed plots were close to streams, and an additional 16 plots were installed along streams for the purpose of the present study. These riparian plots do not strictly follow contour lines because of the gentle downstream slope. The centre-line of each plot was on average 3.5m (SD ±1.12) from the stream margin.

We undertook six surveys with durations between 30 and 35 days each (January–February 2006, March–April 2006, July–August 2006, November–December 2007, April 2008 and July–August 2008). In each survey, we covered all 46 plots. In three surveys we surveyed three plots per day only at night (1830–0200), and in the remaining three surveys we surveyed two plots per day during the day and successively at night (1300–1800 and 1830–0200). The average time of search was 79 minutes per plot (±25.2), with an average walking speed of 208.5m/h (±65.6).

Snakes were recorded using visual searches, exploring the largest possible number of substrates and plant strata for 5 m in the horizontal plane each side of the centre-line of the plot, and 5 m vertically up trees (adapted from Campbell & Christman, 1982). Surveys were undertaken by R. de Fraga and one additional observer.

Environmental variables

Soil samples (30 × 30 × 5cm, free of leaves and roots) were collected in all uniformly distributed plots (six samples collected at intervals of 50 m, pooled for analysis). Clay content was measured in the Department of Agricultural Sciences of INPA. Slope was measured with a clinometer at six points per plot, and average values per plot were used. More details are available at the PPBio website (http://ppbio.inpa.gov.br). Litter depth was measured at 12 equidistant points per plot, and defined as the distance between the highest point of the leaves at the sampling point (every 50 m) and the soil surface, before using mean values per plot.

Stream size and distance measures were obtained in November 2007, in a four-day period with no rain. We measured the distance between each plot to the nearest stream every 50 m along the plot, using the mean for sta-

Table 1. Shapiro–Wilk normality test values for tested variables.

Variables	W	P
NMDS 1	0.96	0.13
NMDS 2	0.97	0.27
NMDS 3	0.99	0.99
NMDS 4	0.98	0.75
Distance from streams	0.69	0.14
Litter depth	0.96	0.21
Percentage clay content	0.96	0.13
Slope of land	0.97	0.27
Stream size	0.83	0.20

Table 2. Individuals per species of snakes found in the Reserva Adolpho Ducke. *N* = total number of individuals, UP = individuals recorded in the uniformly distributed plots, RP = individuals recorded in the riparian plots, URP = individuals recorded in the uniformly distributed riparian plots.

Taxon	*N*	UP (*n*=25)	RP (*n*=16)	URP (*n*=5)
Aniliidae				
Anilius scytale (Linnaeus, 1758)	3	0	1	0
Boidae				
Boa constrictor Linnaeus, 1758	2	1	0	0
Corallus caninus (Linnaeus, 1758)	1	0	1	0
Corallus hortulanus (Linnaeus, 1758)	1	0	0	0
Eunectes murinus (Linnaeus, 1758)	2	0	0	0
Colubridae				
Chironius fuscus (Linnaeus, 1758)	6	0	2	3
Chironius multiventris Schmidt & Walker, 1943	5	2	1	1
Chironius scurrulus (Wagler, 1824)	1	0	1	0
Dendrophidion dendrophis (Schlegel, 1837)	12	7	2	2
Drymoluber dichrous (Peters, 1863)	4	2	2	0
Mastigodryas boddaerti (Sentzen, 1796)	3	0	0	0
Oxybelis fulgidus (Daudin, 1803)	2	0	0	0
Tantilla melanocephala (Linnaeus, 1758)	2	0	0	0
Xenoxybelis argenteus (Daudin, 1803)	13	2	7	3
Dipsadidae				
Atractus latifrons (Günther, 1868)	1	0	0	0
Atractus major Boulenger, 1894	1	1	0	0
Atractus snethlageae Cunha & Nascimento, 1983	1	0	0	0
Atractus torquatus (Duméril, Bibron & Duméril, 1854)	8	0	3	1
Clelia clelia (Daudin, 1803)	3	1	1	0
Dipsas catesbyi (Sentzen, 1796)	1	1	0	0
Drepanoides anomalus (Jan, 1863)	4	0	0	1
Helicops angulatus (Linnaeus, 1758)	3	0	0	0
Helicops hagmanni Roux, 1910	1	0	1	0
Imantodes cenchoa (Linnaeus, 1758)	14	8	0	0
Leptodeira annulata (Linnaeus, 1758)	8	1	3	0
Leptophis ahaetulla (Linnaeus, 1758)				
Liophis reginae (Linnaeus, 1758)	3	0	1	0
Liophis typhlus (Linnaeus, 1758)	3	1	0	0
Oxyrhopus vanidicus Lynch, 2009	1	0	0	0
Philodryas viridissimus (Linnaeus, 1758)	1	0	0	0
Pseudoboa coronata Schneider, 1801	1	0	0	0
Pseudoboa martinsi Zaher, Oliveira & Franco, 2008	3	1	2	0
Siphlophis compressus (Daudin, 1803)		5	1	0
Taeniophallus brevirostris (Peters, 1863)	4	1	0	0
Taeniophallus nicagus (Cope, 1895)	1	0	0	0
Elapidae				
Micrurus averyi Schmidt, 1939	2	2	0	0
Micrurus hemprichii (Jan, 1858)	1	0	0	0
Micrurus lemniscatus (Linnaeus, 1758)	5	0	1	1
Micrurus spixii Wagler, 1824	1	0	0	0
Micrurus surinamensis (Cuvier, 1817)	1	0	0	0
Leptotyphlopidae				
Epictia tenella (Klauber, 1939)	2	0	0	0
Viperidae				
Bothrops atrox (Linnaeus, 1758)	74	6	11	3
Lachesis muta (Linnaeus, 1766)	1	1	0	0

tistical analyses. We measured the width of streams with a measuring tape stretched from one margin to the other at six points located every 50 m along the plot. Stream depth was measured at three equidistant points across the stream depending on the width of the stream, totalling 18 depth measures per plot. The index of stream size used in analyses was the product of mean width and mean depth.

Data analysis

Shapiro–Wilk tests showed that the data are normally distributed (Table 1). Multiple regression models were generated to determine relationships between environmental variables and the number of snake species. Dissimilarities in species composition (presence/absence) were calculated using the Chao index, which is less sensitive to false absences than other indices (Chao et al., 2005). Snake-species composition was summarized by nonmetric multidimensional scaling (*NMDS*) in the R v.5.0 program (http://www.R-project.org), based on the Chao dissimilarities matrix. The configuration produced by four *NMDS* axes was sufficient to explain more than 40% of variance (r^2>0.4) in the original distances.

The scores produced by four *NMDS* axes were used in multivariate multiple regression analyses to determine the influence of environmental variables on species composition. Multivariate axes can only be used in inferential analyses if they are orthogonal (Anderson & Willis, 2003), and there were only negligible correlations (R<0.0003 in all cases) between the axes generated in this study. All the regression models were generated in software Systat 12.

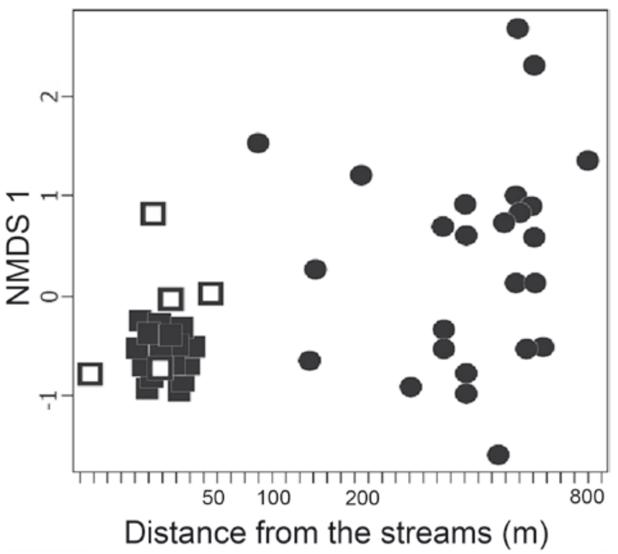

Fig. 3. Values of a one-dimensional *NMDS* axis summarizing snake species composition, along the gradient of distance from the streams, circles=riparian plots, black squares=uniformly distributes plots and open squares=uniformly distributed plots in the riparian zones.

RESULTS

We found 206 snakes belonging to 43 species of seven families (Aniliidae, Boidae, Colubridae, Dipsadidae, Elapidae, Leptotyphlopidae and Viperidae). Sixteen species were found only outside the plots and were not included in the analysis (Table 2). The most commonly encountered species was *Bothrops atrox*, which was recorded in six uniformly distributed and 11 riparian plots (36.9% of plots). *Anilius scytale*, *Atractus major*, *Boa constrictor*, *Chironius scurrulus*, *Corallus caninus*, *Dipsas catesbyi*, *Helicops hagmanni*, *Lachesis muta*, *Liophis reginae*, *L. typhlus* and *Taeniophallus brevirostris* were recorded in only one plot each (2.1%).

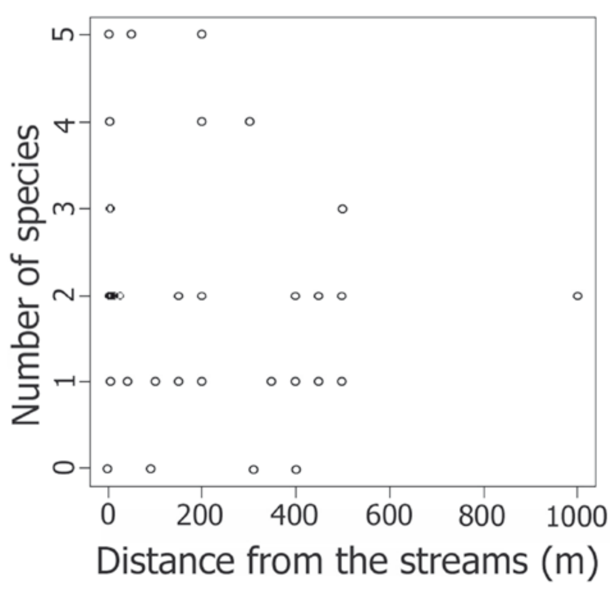

Fig. 2. Relationship between the number of species recorded in individual plots and gradient of distance from the streams (R^2=0.02, P=0.321).

The total number of species recorded in all plots (Fig. 2) was not related to distance from the stream (R^2=0.02, P=0.321). The number of species recorded in all plots, excluding the exclusively arboreal or occasionally terrestrial species (*C. caninus*, *D. catesbyi*, *Imantodes cenchoa*, *Siphlophis compressus* and *Xenoxybelis argenteus*) was not related to litter depth (R^2=0.021, P=0.841). There was evidence that species composition was related to litter depth in the uniformly distributed plots (Pillai trace = 0.517, $F_{4–12}$=3.205, P=0.052), but not to distance from the stream (Pillai trace = 0.23, $F_{4–12}$=0.928, P=0.48), slope of terrain (Pillai trace = 0.39, $F_{4–12}$=1.917, P=0.172) or percentage clay in the soil (Pillai trace = 0.114, $F_{4–12}$=0.386, P=0.815).

The species composition summarized by *NMDS* differed between riparian and uniformly distributed plots (Pillai trace = 0.284, $F_{4–40}$=3.962, P=0.008). Plotting a one-dimensional *NMDS* axis against distance from the streams indicated that species composition has a large range of variation from approximately 100 m away from the streams (Fig. 3). However, some species were detected in several riparian plots, but not in uniformly distributed plots. The direct ordination of presence and absence data

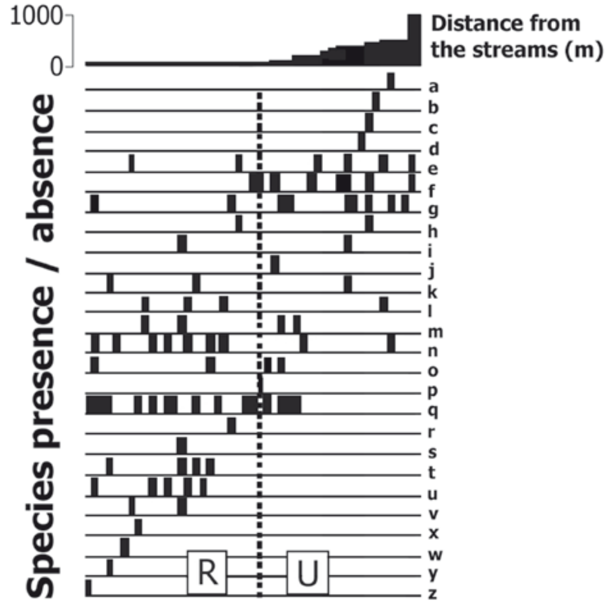

Fig. 4. Direct ordination of presence and absence data for all plots indicating a gradual substitution of species with distance from streams. R = riparian zones, U = uplands. a) *Boa constrictor*, b) *Liophis typhlus*, c) *Dipsas catesbyi*, d) *Lachesis muta*, e) *Siphlophis compressus*, f) *Imantodes cenchoa*, g) *Dendrophidion dendrophis*, h) *Micrurus averyi*, i) *Clelia clelia*, j) *Atractus major*, k) *Pseudoboa martinsi*, l) *Leptodeira annulata*, m) *Drymoluber dichrous*, n) *Xenoxybelis argenteus*, o) *Chironius multiventris*, p) *Taeniophallus brevirostris*, q) *Bothrops atrox*, r) *Liophis reginae*, s) *Drepanoides anomalus*, t) *Atractus torquatus*, u) *Chironius fuscus*, v) *Micrurus lemniscatus*, x) *Helicops hagmanni*, w) *Chironius scurrulus*, y) *Anilius scytale*, z) *Corallus caninus*.

for all plots indicates a gradual substitution of species with distance from streams (Fig. 4). For riparian plots, the size of the stream (Pillai trace = 0.384, F_{4-17}=2.758, P=0.062) and litter depth (Pillai trace = 0.541, F_{4-17}=5.011, P=0.007) were related to snake-assemblage composition.

DISCUSSION

There was no indication of a relationship between the number of species per plot and any of the environmental predictors, and riparian plots did not support more species than non-riparian plots. There does not appear to be a general tendency for higher species richness in riparian zones for snakes (Sabo et al., 2005; this study), although such a tendency has ben observed in other taxa (Emmons & Feers, 1997; Drucker et al., 2008),

Despite harbouring similar numbers of species, the species composition differed significantly between riparian and non-riparian plots independent of litter depth. Although leaf-litter depth apparently affected species composition within both riparian and non-riparian areas, some of the difference in apparent composition could be due to effects of litter on detectability, and more detailed studies will be necessary to understand the causes of the relationship between leaf-litter depth and species composition in Reserva Ducke snakes.

Over large geographic distances, stochastic processes (Hubbell, 2001) and historical influences (Cadle & Greene, 1993; Martins & Oliveira, 1998) greatly affect assemblage composition. However, this study has shown that, even at scales at which these influences are unlikely to affect species turnover, the snake community in Reserva Ducke is affected by local environmental conditions: not all parts of the reserve are equally suitable for all species. High agility and low detectability make it difficult to quantify habitat associations of snakes in studies of individual species with little spatial replication. However, multivariate analyses of assemblages in a large number of sampling sites can reveal distinct patterns of habitat occupation. This approach revealed aspects of habitats selection by snakes that would be impossible to detect with large-scale approaches (Luiselli & Filippi, 2006). Habitat specialization may be even more pronounced than shown by the present study, because snakes are mobile organisms and therefore frequently found in suboptimal habitats while dispersing or moving between foraging or denning patches.

Riparian zones may play different roles for different species; some may be just temporary visitors, while others are permanent residents (Brode & Bury, 1984). In fact snakes in Reserva Ducke respond differently to the gradient of distance from the streams. Some species such as *Drepanoides anomalus* and *Chironius fuscus* appear to have closer relationships with the riparian zone, while other species such as *Dipsas catesbyi* and *Lachesis muta* use areas farther from streams. The distribution of species such as *Drymoluber dichrous* and *Xenoxybelis argenteus* does not depend on the distance from streams. Habitat specialization has been previously reported for snakes (Akani et al., 1999; Heard et al., 2004) and is often expected for tropical species (Jankowski et al., 2009). Reserva Ducke is covered by “terra firme forest”, a superficially homogeneous landscape. Specialities in habitat use can be determined only by the application of refined scales, which define habitats from ecological gradients.

The distinctness of the riparian zone in terms of snake species composition confirms trends found in fish (Pusey et al., 1995), frogs and their tadpoles (Parris, 2004; Rodrigues, 2006; Keller et al., 2009) and understorey herbs (Costa et al., 2005; Drucker et al., 2008). In Brazil, streams of sizes such as those in Reserva Ducke encompass legally protected terrestrial buffer zones of about 30 m (Law nº 4771, 1965, Article 2 of the Federal Forest Code), a standard buffer size used by many jurisdictions around the world (Lee et al., 2004). However, as with understorey plants (Drucker et al., 2008) and birds (Hannon et al., 2002), snakes use riparian zones much wider than this, with the species most associated with riparian zones regularly moving into adjacent areas. Therefore, if the law is enforced in urban and agricultural areas, most of the species associated with riparian zones would be at risk. Despite the fact that each species may occasionally be found in a variety of habitats, large reserves with a mosaic of landscape features, including upland in addition to riparian buffers, may be necessary to the conservation of terrestrial fauna (Semlitsch & Bodie, 2003).

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