Abundance, species richness and diversity of the orb-weaving spider families Araneidae, Nephilidae and Tetragnathidae in natural habitats in Trinidad, West Indies

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ABSTRACT
This study examined the biodiversity of orb-weaving spiders in natural habitats in Trinidad, a continental island with a northern South American fauna. Forty-six localities were sampled, classified into seven formations (representing vegetation structure) and 16 habitat types (based on plant species composition), using visual search and sweep-netting methods, resulting in a total of 1225 individuals of 57 species. Abundance and species richness were significantly related to formation but not habitat type, while both factors influenced species diversity, evenness and dominance. Gamma ($\gamma$) diversity had a larger component of $\beta$ than $\alpha$ diversity did, indicating that between-habitat differences are a substantial part of regional diversity in orb-weaving spiders in Trinidad.

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Araneidae; diversity; Nephilidae; orb-weaving spider; Tetragnathidae

Introduction
There is a general consensus that comprehensive information on the biodiversity of arthropods is lacking at a global level, and the extent of species richness is not known for most taxa (Floren and Deeleman-Reinhold 2005). Spiders are considered to be among the most species-rich animal orders (Coddington and Levi 1991; Foelix 1996). Currently there are 44,906 documented species (Platnick 2014) with an estimated 60,000–170,000 yet to be described (Coddington and Levi 1991). Spiders are good candidates for biodiversity studies as they are relatively easy to identify and can be efficiently sampled in comparison to other invertebrates (Oxborough et al. 2005; Hsieh and Linsenmair 2011), and are sensitive to habitat change (Hsieh et al. 2003). They also occupy a mid-level position in terrestrial food webs as they are major predators of invertebrate populations (Stratton et al. 1979; Wise 1993; Cardoso et al. 2008) but also act as food for organisms at higher trophic levels (Oxborough et al. 2005). Therefore, spiders are suggested to be an important factor in ecosystem stability (Coyle 1981) because they stabilise arthropod populations (Moulder and Reichle 1972; Turnbull 1973; Riechert 1974).
Spider diversity has been well studied in temperate countries but relatively little has been done in tropical regions (Chen and Tso 2004), although those have long been associated with high species richness and diversity (Robinson et al. 1974; Kricher 1989, 2011), particularly tropical rainforests which are among the most diverse and fragile habitats (Wilson 1998). Nevertheless, the tropics comprise a variety of habitats, each with their own characteristic ecology (Bawa and Seidler 1998). The need for information on tropical biodiversity is increased by the accelerating habitat loss such as clearing of forests and savannas and filling in of wetlands (Cardoso 2009). Habitat type is believed to be one of the most important factors influencing arthropod biodiversity, especially with respect to web-building spiders.

This study was conducted on the continental island of Trinidad, which separated from South America at most 10,000 years ago (Kenny 2008), and thus its spider fauna reflects that of the north-eastern part of the continent. This recent separation means that Trinidad shares much of the same biota and climate with close South American countries such as Venezuela and the Guianas. Trinidad’s small size in comparison to the mainland makes it more manageable in terms of sampling. According to the last comprehensive study (Beard 1946), the natural vegetation of Trinidad can be placed into six categories called formations, each of which contains sub-categories termed habitats. Using this classification, a formation is primarily a physiognomic unit containing a floristic association of common structure (i.e., with similar vegetation structure), whereas habitats are more influenced by climatic and edaphic factors and reflect plant species composition. In this study, the biodiversity of spiders that construct orb webs was measured (using several indices) in all the natural habitat types found in Trinidad. Analysis using formation and habitat allowed the relative influence of vegetation structure and plant species composition to be determined.

Methods

Field collection and laboratory analysis

All 15 natural habitat types identified by Beard (1946), plus riparian vegetation, were sampled at 46 localities throughout Trinidad (Figure 1 and Table 1) from March 2006 to May 2009. Brief descriptions of the habitat types are given in Sewlal (2015). Beard’s (1946) classification and description of the vegetation types of Trinidad remains the basis of current work (Helmer et al. 2012), although the distributions have changed with habitats at many localities now being intermediate or disturbed in nature (Baksh-Comeau pers. comm. 2013). The localities used here were selected after consultation with forestry officers and the staff at the National Herbarium, as those least disturbed by human activity such as agriculture or lumber harvesting. Each habitat was studied at three separate localities, except herbaceous swamp and elfin woodland which were both sampled at the only two localities where they occur on the island.

Spiders were collected using two methods (visual search and sweep-netting), which ensured rapid and thorough sampling. Sweep-netting consisted of sweeping understory vegetation and low-hanging branches with a heavy canvas insect net. After
approximately 15–20 sweeps, the net was checked and specimens were transferred to vials containing 70% alcohol, within the confines of the net to prevent loss and escape of specimens. Sweep-netting was not carried out in herbaceous swamp and mangrove woodland habitats as these had no understory vegetation layer. Visual search was carried out in all habitats and consisted of the collector hand-collecting spiders seen with the naked eye. For this method, the surfaces of tree trunks, stems, logs and plants were searched, except in leaf litter and under stones and logs. An assistant was present during data collection but did not participate in the collecting effort or total search time.

Preliminary surveys were carried out at two localities of evergreen seasonal forest and one of deciduous seasonal forest in order to determine the required duration of sampling. Species accumulation curves generated for each locality levelled off after five 3-hour sampling days. Therefore, each locality was sampled for 15 hours, consisting of five samples each of 1 hour sweep-netting and 2 hours visual search (Sewlal and Hailey 2014). A stop watch was used to time each sampling session, which was paused during data collection and recording. The five samples at each locality were at most 1 km apart, and were completed within two weeks in order to reduce the chance of inflating species richness due to transient species. Specimens were identified to the species level with the aid of identification keys (mostly from H.W. Levi; a complete list of the taxonomic works used is given in Sewlal 2010).

Figure 1. Map of Trinidad showing the location of sampling localities of natural habitats.
Table 1. Localities (with codes in parentheses) of formations and habitat types sampled in Trinidad, with global positioning system (GPS) coordinates (UTM).

| Formation          | Habitat type                          | Locality 1 | Locality 2 | Locality 3          |
|--------------------|---------------------------------------|------------|------------|---------------------|
| Seasonal (S)       | Evergreen Seasonal Forest (ESF)       | Arena Forest Reserve (A) (ESF 1 A) | Mt Harris (MH) (ESF 2 MH) | Corammandel (Co) (ESF 3 Co) |
|                    |                                       | 10°33'06.7032"N, -60°11'30.0044"E | 10°30'43.6212"N, -60°06'04.4584"E | 10°07'06.8888"N, -60°14'55.9360"E |
|                    | Semi-evergreen Seasonal Forest (SESF) | Quinam Bay (QB) (SESF 1 QB)     | Trinity Hills (TH) (SESF 2 TH) | Ecclesville (E) (SESF 3 E) |
|                    |                                       | 10°04'30.9468"N, -60°13'02.4260"E | 10°08'45.5532"N, -60°06'56.0520"E | 10°19'08.3028"N, -60°08'38.6376"E |
|                    | Deciduous Seasonal Forest (DSF)       | Mt. St. Benedict (MSB) (DSF 1 MSB) | Mt. St. Benedict (MSB) (DSF 2 MSB) | Chacachacare (Ch) (DSF 3 Ch) |
|                    |                                       | 10°39'43.1244"N, -60°23'44.4444"E | 10°40'42.2580"N, -60°37'26.1264"E | 10°43'31.3716"N, -60°14'45.0544"E |
| Dry Evergreen (DE) | Littoral Woodland (LW)                | Toco (T) (LW 1 T)              | Cap-de ville (Cav) (LW 2 Ca)    | Estuary of Oropouche (EOR) |
|                    |                                       | 10°50'12.6492"N, -60°55'19.5888"E | 10°09'42.2607"E                  | (LW 3 EOR) |
| Montane (Mo)       | Montane Rainforest (MF)               | Lalaja Road (LR) (MF 1 LR)     | Montane Rainforest (MF) (MF 2 MF) | Las Cuevas (C) (MF 3 LC) |
|                    |                                       | 10°25'24.5868"N, -60°09'42.1380"E | 10°43'12.5508"N, -60°16'59.8188"E | 10°47'06.2952"N, -60°23'37.4892"E |
|                    | Lower Montane Rainforest (LMF)        | Heights of Guanapo (HG) (LMF 1 HG) | Cerro del Aripo (CDA) (LMF 2 CDA) | Grande Rivere (GR) (LMF 3 GR) |
|                    |                                       | 10°40'03.9000"N, -60°15'19.0872"E | 10°25'19.4736"N, -60°09'19.5624"E | 10°49'50.1888"N, -60°03'04.9284"E |
|                    | Elfin Woodland (EW)                   | Summit of El Tucuche (SET) (EW 1 SET) | Summit of Cerro del Aripo (CDA) (EW 2 CDA) | – |
|                    |                                       | 10°44'15.0900"N, -60°25'00.6096"E | 10°43'15.5856"N, -60°14'58.6968"E | – |
|                    | Intermediate (I) Seasonal Montane Forest (SMF) | Heights of Aripo (HA) (SMF 1 HA) | Platanal (PI) (SMF 2 PI) | Tureuree Forest (TF) (SMF 3 TF) |
|                    | Swamp (Sw)                            | 10°42'19.7208"N, -60°14'02.4576"E | 10°44'17.5164"N, -60°08'38.6376"E | 10°28'12.9252"N, -60°05'01.7268"E |
|                    | Swamp Forest (SF)                     | Bush Bush (BB) (SF 1 BB)        | Estuary of Oropouche River (EOR) (SF 2 EOR) | Brigand Hill (BH) (SF 3 BH) |
|                    | Palm Swamp (PS)                       | 10°24'04.3524"N, -60°03'20.9952"E | 10°36'50.5584"N, -60°02'29.0832"E | 10°28'12.9252"N, -60°05'01.7268"E |
|                    | Herbaceous Swamp (HS)                 | Bush Bush (BB) (PW 1 BB)        | Los Blanquiales Lagoon (LBL) (PW 2 LBL) | Poole (Po) (PW 3 Po) |
|                    | Mangrove Woodland (MW)                | 10°23'36.9996"N, -60°08'54.7044"E | 10°06'29.8908"N, -60°46'22.2996"E | 10°19'27.7572"N, -60°13'41.4480"E |
|                    | Swamp (Sw) (cont’d)                   | Rousillac Swamp (RS) (HS 1 RS)  | Bush Bush (BB) (HS 2 BB)         | – |
|                    | Marsh Forest (MaF)                    | Caroni Swamp (CS) (MW 1 CS)     | Rousillac Swamp (RS) (HS 1 RS)  | – |
|                    | Savanna (S)                           | 10°13'35.9686"N, -60°33'52.9992"E | 10°29'52.5080"N, -60°03'28.4112"E | – |
|                    | Other (O)                             | Caroni Swamp (CS) (MW 1 CS)     | Caroni Swamp (CS) (MW 1 CS)     | – |
|                    | Riparian Vegetation (RV)              | 10°35'54.6756"N, -60°13'35.2742"E | 10°14'40.9004"N, -60°31'29.4744"E | 10°30'36.3312"N, -60°02'51.3312"E |
|                    | Marshall Forest (MaF)                | Aripo Savanna (AS) (MaF 1 AS)   | Aripo Savanna (AS) (MaF 2 AS)   | Aripo Savanna (AS) (MaF 3 AS) |
|                    | Palm Marsh (PM)                       | 10°35'00.9888"N, -60°12'12.4596"E | 10°37'28.1676"N, -60°11'23.3232"E | 10°36'35.7516"N, -60°12'00.0216"E |
|                    | Savanna (S)                           | Aripo Savanna (AS) (PM 1 AS)    | Aripo Savanna (AS) (PM 2 AS)    | Aripo Savanna (AS) (PM 3 AS) |
|                    | Other (O)                             | Aripo Savanna (AS) (S 1 AS)     | Aripo Savanna (AS) (S 2 AS)     | Aripo Savanna (AS) (S 3 AS) |
|                    | Riparian Vegetation (RV)              | 10°35'00.9132"N, -60°12'12.3048"E | 10°38'31.0140"N, -60°11'26.7288"E | 10°36'49.6476"N, -60°12'02.8800"E |
|                    |                                    | Caura River (CV) (RV 1 CV)      | Poona (P) (RV 2 P)              | Vessigny (V) (RV 3 V) |
|                    |                                    | 10°41'16.5696"N, -60°22'18.6996"E | 10°20'32.2008"N, -60°22'55.1604"E | 10°14'04.2684"N, -60°37'25.2768"E |
Data analysis

Species accumulation curves (cumulative number of observed species over the five samples) were constructed for each locality. The observed species richness (S) was the total after the five samples. Nine separate species richness estimators were calculated, using the program EstimateS 8.0 (Colwell 2006). The median of these nine values was found to be the most robust measure of estimated species richness (E) for each locality, as described in detail by Sewlal and Hailey (2014). The present paper gives data on the abundance of individuals and the observed and estimated species richness for the natural habitats, and analysis by formation and habitat type.

Three diversity indices were calculated: Shannon-Wiener ($H'$) which measures species diversity, Simpson ($D$) which measures evenness and Berger-Parker ($d$) which measures dominance (Magurran 2004), as follows: (1) $H' = -\sum p_i \ln p_i$, where $p_i = n_i/N$ (the abundance of species $i$ at a locality as a proportion of the total sample at that locality); (2) $D = 1/y$, where $y = \sum [n_i (n_i - 1)/N(N - 1)]$. The Simpson index was thus used in reciprocal form, as recommended by Downie et al. (1995) and Magurran (2004) to give a measure directly related to diversity. The two alternative forms of the Simpson index, $-\ln y$ and $1 - y$ (Magurran 2004), both yielded non-normal distributions that were not transformable because of multiple peaks; (3) $d = n_{\text{max}}/N$, where $n_{\text{max}}$ is the number of individuals of the most common species. Niche breadth ($B$) for habitat was calculated for each species as $B = 1/\Sigma p_i^2$ where $p_i = n_i/N_s$ (the abundance of the species at locality $i$ as a proportion of the total sample of that species) (Pianka 1973). The mean niche breadth was then calculated at each locality, averaging across the species present at that locality.

The habitats were grouped according to vegetation structure into six formations after Beard (1946): since riparian vegetation was not included or classified by Beard (1946), it is designated as a seventh, ‘other’, formation. Two-way generalized linear models analysis of variance (ANOVA) tests were carried out with formation, and habitat nested within formation, allowing both levels to be assessed simultaneously for their effects on spider abundance and diversity. The data were first checked for normality using the Anderson Darling normality test. If the data were significantly non-normal the test was carried out on transformed data using squares, square roots or logarithms as appropriate (Sewlal 2013). Statistical analysis used Minitab (14 or 15) and Statistix 7.

Results

Abundance

Sampling yielded a total of a total of 1225 individuals of 57 orb-weaving species (listed by Sewlal 2013), out of the 89 species recorded from Trinidad (Sewlal 2010). They included eight new and unidentified species of araneids, nine species of tetragnathids including a new species, and a single species of nephilid (Sewlal 2013). Abundance averaged 26.6 individuals per locality, ranging from means of 10.5 for localities of elfin woodland to 75.0 for localities of savanna (Table 2). A nested ANOVA showed that abundance was significantly influenced by formation but not by habitat type (Table 3).
Table 2. Mean and range for abundance (N), observed species richness (S), estimated species richness (E), Shannon index (H'; species diversity), Simpson index (D; species evenness), Berger-Parker index (d; dominance) and niche breadth of species present (B) across the localities for each of the natural habitats in Trinidad.

| Formation     | Habitat      | N      | S       | E       | H'      | D       | d       | B       |
|---------------|--------------|--------|---------|---------|---------|---------|---------|---------|
| Seasonal (S)  | ESF          | 34.3 (23–49) | 9.0 (8–11) | 14.2 (9.1–23.2) | 1.86 (1.84–1.89) | 6.2 (5.1–7.2) | 0.31 (0.29–0.34) | 7.2 (6.4–8.8) |
|               | SESF         | 16.7 (3–29)  | 5.0 (2–7)  | 7.7 (3.0–12.7) | 1.25 (0.63–1.59) | 4.1 (3.0–5.5) | 0.46 (0.33–0.67) | 6.1 (3.2–8.9) |
|               | DSF          | 44.0 (33–61) | 11.0 (9–14) | 18.2 (13.2–25.7) | 1.90 (1.59–2.24) | 5.9 (3.5–8.0) | 0.35 (0.27–0.50) | 6.2 (5.1–7.4) |
| Dry evergreen (DE) | LW         | 15.3 (5–33)  | 2.0 (1–4)  | 2.5 (1.0–5.6) | 0.19 (0.00–0.58) | 1.1 (1.0–1.4) | 0.95 (0.85–1.00) | 6.7 (2.4–9.4) |
|               | SESF         | 16.7 (3–29)  | 5.0 (2–7)  | 7.7 (3.0–12.7) | 1.25 (0.63–1.59) | 4.1 (3.0–5.5) | 0.46 (0.33–0.67) | 6.1 (3.2–8.9) |
|               | DSF          | 44.0 (33–61) | 11.0 (9–14) | 18.2 (13.2–25.7) | 1.90 (1.59–2.24) | 5.9 (3.5–8.0) | 0.35 (0.27–0.50) | 6.2 (5.1–7.4) |
| Montane (Mo)  | LMF          | 20.0 (15–23) | 7.7 (4–11)  | 10.8 (5.6–18.5) | 1.63 (0.95–2.18) | 6.0 (2.2–10.5) | 0.43 (0.22–0.67) | 7.7 (6.9–8.6) |
|               | MF           | 22.3 (18–33) | 9.3 (7–13)  | 18.2 (8.0–38.0) | 1.89 (1.31–2.47) | 12.3 (2.8–25.5) | 0.33 (0.17–0.58) | 8.0 (6.0–9.0) |
|               | EW           | 10.5 (8–13)  | 4.5 (4–5)  | 5.6 (4.7–6.4) | 1.41 (1.27–1.55) | 6.6 (3.9–9.3) | 0.36 (0.25–0.46) | 9.3 (8.6–9.9) |
| Intermediate (I) | SMF       | 14.7 (5–28)  | 6.0 (4–9)  | 8.9 (6.0–12.8) | 1.56 (1.33–1.87) | 7.3 (5.9–10.0) | 0.34 (0.27–0.40) | 9.4 (8.9–9.8) |
| Swamp (Sw)    | SF           | 16.7 (9–23)  | 7.3 (4–10)  | 13.9 (5.8–25.8) | 1.75 (1.36–2.13) | 7.7 (5.4–11.8) | 0.31 (0.22–0.39) | 7.6 (7.0–8.7) |
|               | PS           | 17.3 (14–20) | 7.0 (6–8)  | 9.1 (8.3–10.0) | 1.97 (1.64–2.41) | 8.4 (6.5–10.2) | 0.29 (0.22–0.35) | 8.1 (6.3–10.0) |
|               | HS           | 13.0 (10–16) | 2.0 (1–3)  | 2.3 (1.0–3.7) | 0.45 (0.00–0.90) | 1.7 (1.0–2.3) | 0.82 (0.63–1.00) | 10.1 (7.8–12.4) |
|               | MW           | 21.3 (9–46)  | 3.3 (1–6)  | 6.3 (1.0–14.0) | 0.89 (0.00–1.67) | 4.3 (1.0–9.0) | 0.57 (0.33–1.00) | 5.7 (2.4–10.4) |
| Marsh (Ma)    | MaF          | 45.7 (20–89) | 11.0 (9–14) | 15.1 (14.6–15.5) | 2.26 (1.92–2.72) | 10.8 (6.6–13.9) | 0.25 (0.20–0.32) | 7.2 (6.0–8.8) |
|               | PS           | 28.3 (12–54) | 9.3 (5–15)  | 13.8 (6.6–20.6) | 1.88 (1.51–2.27) | 8.8 (6.0–7.1) | 0.33 (0.33–0.35) | 8.5 (7.0–10.3) |
|               | S            | 75.0 (50–114)| 6.7 (4–10)  | 8.1 (4.5–13.2) | 1.23 (0.84–1.79) | 2.9 (1.8–4.8) | 0.57 (0.34–0.72) | 5.8 (5.2–6.4) |
| Other (O)     | RV           | 21.0 (4–46)  | 7.3 (3–11)  | 10.0 (4.6–15.0) | 1.59 (1.03–1.92) | 6.7 (4.4–9.8) | 0.42 (0.31–0.50) | 5.9 (5.6–6.2) |
| Mean          | Locality     | 26.6        | 6.9       | 10.6      | 1.51      | 6.3       | 0.44      | 7.4       |
| Total         | Trinidad     | 1225        | 57        | 65.2      | 3.22      | 17.7      | 0.11      | 3.5       |

Notes: Habitat abbreviations as in Table 1. ESF, Evergreen Seasonal Forest; SESF, Semi-evergreen Seasonal Forest; DSF, Deciduous Seasonal Forest; LW, Littoral Woodland; LMF, Lower Montane Rainforest; MF, Montane Rainforest; EW, Elfin Woodland; SMF, Seasonal Montane Forest; SF, Swamp Forest; PS, Palm Swamp; HS, Herbaceous Swamp; MW, Mangrove Woodland; MaF, Marsh Forest; PM, Palm Marsh; S, Savannah; RV, Riparian Vegetation.
Species richness

Observed species richness increased significantly with abundance among samples at the 46 localities, but little of the variation in species richness was explained simply by the numbers of individuals ($r^2 = 20\%$; Figure 2). Observed species richness at a locality averaged 6.9, with habitat means ranging from 2.0 in littoral woodland and herbaceous swamp to 11.0 in deciduous seasonal woodland and marsh forest (Table 2). Sampling efficiency (observed/estimated species richness) was 57% in natural habitats, and did not vary significantly among them; there was also a strong correlation ($r^2 = 74\%$) between estimated and observed species richness (Sewlal and Hailey 2014). Estimated species richness averaged 10.6 per locality, with habitat means ranging from 2 to 3 in littoral

![Figure 2](image-url)
woodland and herbaceous swamp to over 18 in deciduous seasonal forest and montane forest (Table 2). Nested ANOVA tests showed that formation (vegetation structure) had a greater influence than habitat (plant species composition) did on both observed and estimated species richness, but only the effect of formation on observed species richness was significant (Table 3).

**Species diversity indices**

Habitats with little or no canopy cover (so that the vegetation is subjected to harsh environmental conditions) had low diversity and evenness values: littoral woodland, savanna and herbaceous swamp \(H' < 1.3, D < 3.0; \text{Table 2}\). These habitats also had high dominance \(d > 0.5\). Marsh forest had the highest average diversity value \(H' = 2.26, D = 10.8\).

Nested ANOVA tests showed that both formation and habitat had independent and similarly significant effects on diversity, evenness and dominance (Table 3). When transformed (as in Table 3), species evenness \(D\) was strongly correlated with species diversity \(H'\) \(r^2 = 72\%\), while dominance \(d\) showed a strong negative correlation with species diversity \(r^2 = 67\%\).

**Niche breadth**

The mean habitat niche breadth of the 57 species of orb-weaving spiders found in natural habitats was 3.5 (Table 2). The mean habitat niche breadth of species at each locality, averaged within habitats, was higher, because species with higher niche breadth contributed to samples at more localities. The mean habitat niche breadth of species at each locality ranged from 5.7–5.9 in mangrove woodland, savanna and riparian vegetation, to 9.3–10.1 in elfin woodland, seasonal montane forest and herbaceous swamp (Table 3). Overall, there was relatively little variation in mean habitat niche breadth of species among habitats, and this was not significantly related to either formation or habitat type (Table 3).

There was no correlation between mean niche breadth of species at a locality and observed species richness (Figure 3), or with estimated species richness or the three measures of diversity (transformed as in Table 3; unsigned \(r\) values all \(< 0.14, P > 0.35\)). Localities with high species richness thus did not have many species mostly because of the presence of many generalists, or the division of the total niche space by many specialists, but because of a combination of both generalists and specialists.

**Analysis of diversity**

Values of diversity per locality in Table 2 correspond to local or \(\alpha\) diversity, and the total for all natural habitats in Trinidad corresponds to a regional or \(\gamma\) diversity. It is thus possible to show how variation between habitats contributes to total regional diversity, as \(\beta\) diversity = \(\gamma/\alpha\) (Tuomisto 2010). The Shannon index was converted to an effective species equivalent for this calculation, as \(e^{H'}\) (Krebs 1999); the Simpson index in the form \(D\) as used here is already an effective species equivalent (Krebs 1999). Beta diversity values are thus 57/6.9 = 8.3 for observed species richness, 65.2/10.6 = 6.2 for estimated species richness, 25.0/5.4 = 4.6 for the Shannon index and 17.7/6.3 = 2.8 for the Simpson index.
Discussion

Habitat structure has been stated as a major factor influencing species richness and abundance of spiders (Stratton et al. 1979; Hatley and MacMahon 1980; Halaj et al. 1998; Peres et al. 2007). Therefore, habitat structure should be considered one of the most important factors influencing the richness and composition of spider assemblages in tropical forests, as it indicates that more diverse microclimates are present (Uetz 1991), and also influences the amount of rain and light that reach the forest floor, thereby creating many different substrate types (Loyola and Martins 2009).

The results for orb-weavers in Trinidad show that formation has a greater effect on abundance of individuals and species richness than habitat type does; therefore, vegetation structure rather than plant species composition is the main influencing factor with respect to biodiversity among the natural habitats. Structural aspects that have been recorded in the literature to influence the presence of web-building spiders include space and attachment points for web construction (Duffey 1962; Cherrett 1964; Riechert and Gillespie 1986; Uetz 1991), protection from thermal extremes (Riechert and Gillespie 1986) and protection for the web itself (Enders 1974, 1977; Hodge 1987).

Species richness is not the only component of biodiversity. The importance of the measurement of species diversity has become critical to understanding tropical communities and for their conservation in the face of global destruction of tropical forests (DeVries et al. 1997). In contrast to species richness, both formation (vegetation structure) and habitat (plant species composition) influenced species diversity, evenness and

Figure 3. The absence of a relationship between mean niche breadth of species and observed species richness at a locality, for 46 localities with natural habitats; \( r = -0.12, P = 0.42 \).
dominance of orb-weaving spiders. Plant composition influences microhabitats, for instance the presence of buttress roots in evergreen seasonal forest. The space between buttress roots (referred to as ‘buttress notches’) has been noted as a microhabitat that contains a very high biodiversity of web-building spiders (Huber 2000). Buttress notches act as suitable microhabitats as they can provide protection from predators and the elements (Sewlal 2009), and can potentially contain a relatively stable microclimate.

Results from this study are comparable to the few previous studies of spider diversity. Tsai et al. (2006) found a total of 78 species of spiders in natural forest on Orchid Island, Taiwan, with $H' = 2.36$ and $D = 1.16$. Coyle (1981) found 60 species in rock forest habitat (Tennessee and North Carolina, USA), with $H' = 3.17$. Other studies are more comparable to single localities recorded here. Thus, Bultman et al. (1982) found 11 species of spiders in beech-maple climax forest in Tennessee and North Carolina, USA, with $H' = 2.31$; and Jetton et al. (2009) found 7–10 species in two localities of old growth forest in Great Smoky Mountains National Park, Tennessee and North Carolina, USA, with $H' = 0.49–0.83$.

Regional ($\gamma$) diversity was made up more by between-habitat than by within-habitat diversity (that is, $\beta > 2$ for all variables, and ranging up to 8.3 for observed species richness). Although rainforest is the common example of high diversity in tropical areas, this study shows that differences among habitats are highly important for total regional diversity. Conservation work therefore should not focus exclusively on tropical rainforest, at least for this guild of spiders. The habitats in formations are grouped by physiognomy, and these formations may have a very wide distribution throughout the American tropics (Beard 1946), so that the factors dominating diversity found in Trinidad can also be applied to the nearby South American continent.

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