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The lizard community of a subtropical dry forest: Guánica forest, Puerto Rico

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Abstract: Globally, dry forests represent a threatened ecosystem, and documentation of biodiversity in the few remaining remnants of dry forest is needed as a basis for conservation planning. Guánica forest, one of the best remaining representatives of subtropical dry forest habitat, supports the richest, and most complete native dry forest lizard community on the island of Puerto Rico. The lizard community there is comprised of 10 species, some of which are differentially distributed among coastal scrub, deciduous, and semi-evergreen forest. *Anolis cristatellus* and *Sphaerodactylus nicholsi* are the most abundant in all forest types, while *Anolis cooki*, a threatened species, is restricted to coastal scrub habitat. *Sphaerodactylus nicholsi* was most abundant in habitats where leaf litter was deep, especially in humid ravines. These data on lizard community composition and abundance in a relatively undisturbed dry forest provide insights into dry forest community ecology and a reference against which other dry forest lizard communities in disturbed or otherwise impacted habitats can be compared.

Resumen: A nivel mundial los bosques secos representan un ecosistema amenazado, y el registro de la biodiversidad en los pocos remanentes de bosque seco es necesario como una base para planear su conservación. El bosque Guánica, uno de los mejores ejemplos que todaví se conservan del habitat de bosque seco subtropical, mantiene la comunidad más rica y más completa de lagartijas natives de bosque seco en la isla de Puerto Rico. La comunidad de lagartijas en este sitio está compuesta por 10 especies, algunas de las cuales está distribuida de manera diferencial entre el matorral costero, y los bosques deciduo y subperennifolio. *Anolis cristatellus* y *Sphaerodactylus nicholsi* son las más abundantes en todos los tipos de bosque, mientras que *Anolis cooki*, una especie amenazada, está restringida al habitat de matorral costero. *Sphaerodactylus nicholsi* fue más abundante en habitats donde el mantillos foliar era profundo, especialmente en cañadas húmedas. Estos datos de abundancia y composición de la comunidad de lagartijas en un bosque seco relativamente no perturbado proporcionan una nueva apreciación de la ecología de comunidades de bosque seco y una referencia para comparar otras comunidades de lagartijas de bosques secos en habitats perturbados o con algún otro tipo de impacto.

Resumo: Globalmente, as florestas secas representam um ecossistema ameaçado, pelo que a documentação sobre a sua biodiversidade, nas poucos áreas restantes é necessária como base para o planeamento da conservação. A floresta de Guanica, uma das melhores parcelas mais representativa do que resta do habitat florestal seco subtropical, suporta a comunidade de lagartos nativos mais rica da floresta seca compreendendo 10 espécies, alguns dos quais estão diferencialmente distribuídos ao longo da zona de mato costeiro, da zona de floresta decídua, e semi-sempreverde. A *Anolis cristatellus* e *Sphaerodactylus nicholsi* são as mais abundantes em

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todos os tipos florestais, enquanto que a *Anolis cooki*, uma espécie ameaçada, se encontra restrita ao habitat de mato costeiro. A *Sphaerodactylus nicholsi* era a espécie mais abundante nos habitats com maior espessura de folhada, especialmente nas ravinas húmidas. Estes dados sobre a composição da comunidade de lagartos, e sobre a sua densidade, numa floresta seca relativamente intacta, proporcionam um conhecimento aprofundado sobre a ecologia da comunidade da floresta seca e uma referência contra as quais outras comunidade de lagartos em florestas secas, em habitats disturbadas ou de qualquer forma com habitats afectados, podem ser comparadas.

Keywords: *Ameiva, Anolis*, community ecology, Guánica forest, lizards, *Phyllodactylus*, Puerto Rico, *Sphaerodactylus*, subtropical dry forest.

Introduction

Dry forest ecosystems are globally threatened throughout the tropics (Janzen 1988a,b; Murphy & Lugo 1990; Redford *et al.* 1990), and documentation of biodiversity in the few remaining large intact tracts of dry forest is needed as a basis for conservation planning in these threatened regions. Dry forests are more subject to disturbance than other forest types as a result of the comfortable climate and relatively rich soils, factors which tend to promote high human populations (Lerdau *et al.* 1991; Redford *et al.* 1990). Disturbance and forest clearing are continual threats to dry forest and their resident fauna and flora; forest cover in Puerto Rico was reduced from 95% in pre-colonial times to 5% in 1948 (Birdsey & Weaver 1982). Since then, forest cover has been increasing as abandoned lands have been allowed to revert back to successional forests (Birdsey & Weaver 1987; Lugo *et al.* 1996). Guánica forest is the best remaining example of dry forest habitat in Puerto Rico (Murphy & Lugo 1995), and ecosystems such as this can serve as an important reference system for other protected dry forests, forests that remain only as fragmented remnants, and converted lands.

Lizards are ubiquitous inhabitants of subtropical and tropical regions. Past surveys of the island of Puerto Rico have recorded 33 (Rivero 1978) to 43 (Schwartz & Henderson 1991) species on the main island and the surrounding smaller islands and cays. Within this diverse assemblage, 13 species (eight of which are endemic to Puerto Rico and the Virgin Islands) are represented in the subtropical dry forest life zone (*sensu* Holdridge 1967). Three of these species were not encountered during this study as a result of their restricted habitat requirements, small population sizes, and/or limited distribution throughout the region (Table 1, Rivero 1978; Schwartz & Henderson 1991). Along with frogs, snakes, and some birds, lizards are important carnivores, occupying the higher trophic levels in tropical forested ecosystems (Reagan 1996; Stewart & Woolbright 1996; Thomas & Gaa Kessler 1996). Any perturbation in their community composition or population density have the potential to affect the entire ecological community (e.g., Reagan 1991; Woolbright 1991).

Anolis lizards are very conspicuous and wide-

Table 1. Families and species of lizards represented in the dry forest zone of Southwestern Puerto Rico (compiled from Rivero 1978; Schwartz & Henderson 1991).

Polychridae	Teiidae	Gekkonidae	Scincidae
Anolis cristatellus	◦*Ameiva exsul*	◦*Sphaerodactylus nicholsi*	**Mabuya mabouya*
◦*Anolis cooki*	◦*Ameiva wetmorei*	◦*Sphaerodactylus roosevelti*	
◦*Anolis stratulus*		**Sphaerodactylus macrolepis*	
◦*Anolis pulchellus*		*Phyllodactylus wirshingi*	
◦*Anolis poncensis*		**Hemidactylus brooki*	

* species which are rare or patchily distributed and not encountered during this study.
◦ species endemic to the Puerto Rican Island Bank (Puerto Rico, Virgin Islands, and surrounding islets and cays).

spread vertebrates in Caribbean terrestrial ecosystems (Moermond 1979; Williams 1969, 1976). These lizards are diurnal, primarily insectivorous, and are ecologically distributed along a vertical gradient from ground level to forest canopy throughout virtually every habitat type in Puerto Rico (Rand 1964). Of the five species of *Anolis* found in the dry forest life zone, three are widely distributed across the island (*Anolis cristatellus* Duméril & Bibron, *Anolis pulchellus* Duméril & Bibron, and *Anolis stratulus* Cope), while the other two are restricted to the arid southwestern coastal region (*Anolis poncensis* Stejneger and *Anolis cooki* Grant) (Rivero 1978; Schwartz & Henderson 1991). Two species of *Ameiva* are found in southwestern Puerto Rico: *Ameiva exsul* (Cope), which is abundant in open or disturbed habitats in the lowlands around the entire perimeter of the island (Heatwole & Torres 1967; Schwartz & Henderson 1991), and *Ameiva wetmorei* (Stejneger), which is found only in the dry forest life zone (Rivero 1978; Schwartz & Henderson 1991). The three geckos commonly encountered during this study, *Sphaerodactylus nicholsi* (Grant), *S. roosevelti* (Grant), and *Phyllodactylus wirshingi* (Kerster & Smith), are all restricted to dry coastal areas (Schwartz & Henderson 1991; Thomas & Schwartz 1966).

Although some assemblages or individual species of dry forest lizards have been studied in Puerto Rico (e.g., Hass 1991; Jenssen *et al.* 1984; Lewis 1986, 1989; Lewis & Saliva 1987; Marcellini *et al.* 1985; Ortiz & Jenssen 1982), community composition and species abundance have not been documented for many locations. Thus, we undertook a study that would establish abundance, distribution, and important ecological relationships among dry forest lizard species in a relatively undisturbed dry forest in southwestern Puerto Rico. The resulting data can be used as a reference for conservation planning in southwestern Puerto Rico as well as for lizard communities in other dry forest regions. We addressed the following questions in this study: (1) What are the distributions of dry forest lizard species in Guánica forest, a protected dry forest? (2) What patterns of relative abundance and community dominance among lizard species are found? (3) How does the lizard community (i.e., diversity, evenness, and community similarity) compare among habitat types within Guánica forest (coastal scrub, deciduous and semi-evergreen forest)? (4) What structural features of the habitat help to explain species and community patterns?

Materials and methods

Study region

The dry forest life zone of southwestern Puerto Rico encompasses an area of approximately 121,640 hectares (ha) extending 120 km eastward from Cabo Rojo on the extreme southwestern corner of the island, and the northern boundary of the dry zone ranges from 3-20 km inland, depending upon local topography (Fig. 1 inset, Ewel & Whitmore 1973). The vast majority of Puerto Rico's dry forest habitat occurs in this region. Dry forests are also found along the northeastern coast of Puerto Rico and constitute the predominant life zone on all surrounding islands (Ewel & Whitmore 1973), although only approximately 4% of the original forested area remains (Murphy & Lugo 1990; Murphy *et al.* 1995). The balance of dry forest habitat has been converted to agricultural and developed land.

The dry zone in the southwestern region of the island lies in the rain shadow of the Cordillera Central, and receives between 600-1100 mm of precipitation annually, which varies with location and seasonality (Ewel & Whitmore 1973). Most of the rainfall occurs in either the longer wet season from August until November or the shorter wet season during the month of May, however, timing and duration of seasons and rainfall are highly variable from year to year (Murphy & Lugo 1990, 1995).

Guánica commonwealth forest

Guánica forest is situated roughly at the center of the dry zone's east-west orientation, where it receives approximately 860 mm of rainfall annually (Ewel & Whitmore 1973; Murphy & Lugo 1990). The area was designated a Commonwealth forest in 1917, and has been protected and managed to varying degrees since the 1930's. In 1982, protection and management efforts were increased when Guánica forest became a Biosphere Reserve in the UNESCO Man in the Biosphere program.

Guánica forest currently encompasses approximately 4000 ha, a significant increase from the original 2079 ha reserve (Lugo *et al.* 1996). This area has been subjected to a wide variety of

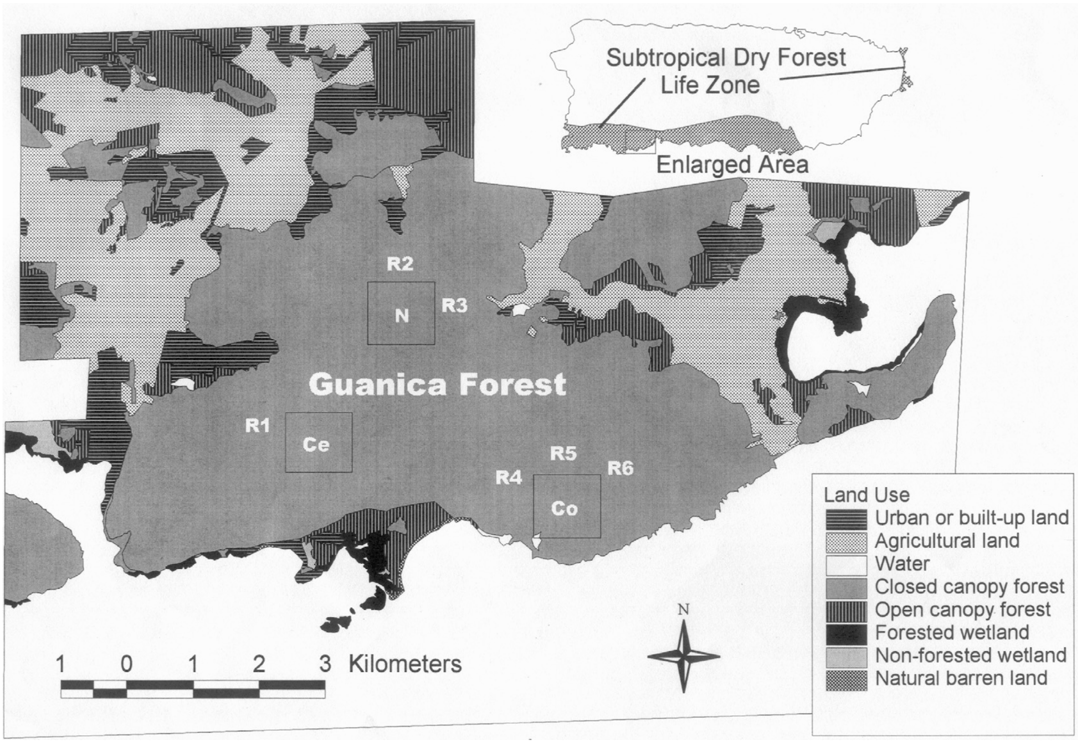

Fig. 1. Land use map of Guánica forest (eastern section) and vicinity. Study sites within the reference forest are labeled as follows: Co=coastal scrub, Ce=central site of upland forest on predominantly south-facing slopes, N=northern site of upland forest on predominantly north-facing slopes, R1-R6 = ravines.

activities and uses throughout its history, including tree plantations (*Haematoxylum campechianium* and *Swietenia mahogani*), charcoal and fence post production, agriculture (both cultivated crops and livestock), and human settlements (Murphy *et al.* 1995). Most of these activities ceased by the 1930's or 1940's, but fencepost harvesting continued until the 1970's (M. Canals Mora, pers. comm.).

Guánica forest is divided into two sections, separated by Guánica Bay. The western portion is a smaller, more recently acquired, and less intensively managed tract than the eastern portion. The eastern tract contains the original forest reserve, which has been protected since the 1930's. The entire forest supports a wide array of vegetation types and associations, with three primary categories: coastal scrub, deciduous forest, and semi-evergreen forest. An additional feature of Guánica forest is an extensive cave system that has resulted from dissolution of underlying limestone. Collapsed cave systems now form narrow ravines and canyons along a north-south orientation in the forest. These ravines and canyons often flood in the wet seasons and during large storms, and support flora and fauna in a more mesic environment as compared to adjacent uplands (Farnsworth 1993).

Site selection

Three 1 km x 1 km blocks and six ravines were selected as study sites within the protected, contiguous eastern portion of Guánica forest for this study (Fig. 1). Criteria for site selection included representation of vegetation type (coastal scrub, deciduous forest, or semi-evergreen forest), accessibility, and disturbance history. In the sites that were selected, each primary vegetation association was represented, and within the deciduous forest type areas that had been disturbed since 1936 were selected as well as those with no record of disturbance in the same time period (Lugo *et al.* 1996). Each site measured 100 ha (with the exception of the ravines, discussed below), and was delineated using topographic maps (USGS quandrangles: Guánica and Punta Verraco). The sites within Guánica forest included a coastal scrub (Co, Fig. 1) along the southern coast and two upland deciduous forest sites in the central and northern section of the forest. The central site (Ce, Fig. 1) included predominantly south-facing slopes, while the slopes in the northern site (N, Fig. 1) were primarily north-facing. The two deciduous forest sites also differed in their history of human disturbance; the central site has suffered minimal disturbance over the past 60 years while the northern site is a mixture of recovering and relatively unimpacted forest stands (Vélez-Rodriguez 1995 a-f). Six ravines (R1-R6, Fig. 1), representing semi-evergreen forest, were selected for sampling from topographic maps and personal observations based on the site selection criteria discussed above; these sites did not constitute a continuous 100 ha tract as did the others; rather, the number of ravines was selected to match the sampling regime for each of the other sites (Table 2).

Sampling methods

Due to differences in the biology and activity patterns of the 10 commonly encountered dry forest lizard species, two sampling strategies were required to obtain accurate estimates of diversity and abundance. Arboreal or free-ranging *Anolis* and *Ameiva* lizards are conspicuous diurnal species. Species in these genera were censused along 100 m transects of fixed area (modified belt transects, discussed below). *Sphaerodactylus* and *Phyllodactylus* geckos are primarily nocturnal and/or fossorial. These species were sampled by carefully searching through litter and ground debris in 2 m x 2 m plots (Table 2).

Lizard surveys were conducted along randomly located 100 m transects in each of the study sites during the summers of 1997 and 1998. Sampling locations within these sites were determined randomly with a point grid overlain on the 100 ha site map. Coastal, central, and northern sites were sampled in May-August, 1997. These were resampled and ravines were added to the study in July-August, 1998. In the field, the transect locations were determined with the aid of topographic maps, a compass, and landmarks. When site topography allowed, sampling locations were stratified using four aspect categories (N-, S-, E-, and W-facing slopes). Six 100 m transects were established in each of the three 100 ha sites, while one transect per ravine was established in each of the six ravines (Table 2).

Each 100 m transect ran perpendicular to the slope, and was subdivided into circular sample plots at 5 m intervals. Lizards were censused by slowly walking along the fixed-area transect and stopping at the center of each plot to identify and count the individuals within a 2.5 m radius. Methods used in this study were modifications of techniques utilized by Reagan (1992), whose methods were based on the Frye strip census method (Overton 1971). A fixed area transect was used to improve the accuracy of the area estimation, since visually estimating angles or distances to individuals can be imprecise (Heckel & Roughgarden 1979).

Each of the circular transect plots was carefully surveyed visually until all individuals had been detected (approximately 5 minutes, but duration was highly dependent on structural diversity and density of the vegetation). All transects were surveyed by a single observer (K.S.G.) to eliminate any observer bias. The location (i.e., perch) of each lizard was recorded to ensure that no lizards were counted more than once, and each transect was surveyed twice to ensure that all individuals were counted.

Table 2. Summary of sampling design in Guánica Commonwealth Forest.

Site ID	Area (ha)	Total area of transects (m^2)	Number of 10 m x 10 m plots♀	Number of 2 m x 2 m plots	Site walk#
Coastal (Co)	100	2520 (6)	8	24	Yes
Central (Ce)	100	2520 (6)	8	24	Yes
North (N)	100	2520 (6)	8	24	Yes
Ravines (R)	*	2520 (6)	6	18	No

♀ Located at the beginning of each transect and additional randomly established individual plots

Presence/absence data only for sites sampled in both 1997 and 1998.

* Ravines were not continuous 100 ha, rather six individual ravines were selected to match the sampling design of the other three sites.

Adult *Anolis* lizards exhibit remarkable fidelity to their perch and territory (Philibosian 1975; Rand 1964), and the second survey of the transect was made within a few hours to account for diurnal differences in activity and abundance (Reagan 1986). This two-survey method yielded more accurate counts of individuals in the sampling area than those obtained from one survey alone.

At the beginning of each transect, a 10 m x 10 m plot was established, within which three 2 m x 2 m subplots were randomly selected. Because the area sampled with 10 m x 10 m plots was substantially less than the sampled with the transect methods, two additional 10 m x 10 m plots were also randomly established within each site, with the exception of the ravines (Table 2). Plot sampling accounted for less total area sampled than transect sampling because of the greater time investment involved in careful searches of subplot.

Each subplot was thoroughly searched for geckos by examining and clearing away all leaf litter and overturning all rocks to investigate potential refuges within the substrate. After each plot was searched, all litter and rocks were replaced to minimize impacts on substrate habitat. The following data were recorded for each subplot: (1) species identification of each individual, (2) number of individuals of each species, (3) percent rock cover, and (4) average litter depth (cm). Percent rock was visually estimated, and litter depth was determined by taking the mean of three random measurements within each subplot prior to clearing the litter.

In addition to the quantitative transect and plot sampling methods described above, qualitative focal searches (site walks) of study sites sampled in 1997 were made during the summer of 1998 to ensure that all species present were recorded for each site. A species list was considered complete if all ten dry forest lizard species were present at any given site. Site walks yielded only presence/absence data, and were conducted only at sites with incomplete species lists.

Data analysis

For both transect and plot sampling methods, population density and relative abundance of each species were calculated. Community metrics were also calculated from the density and relative abundance data, including community similarity, diversity, and evenness. Data from the sites that were resampled in 1998 were used to test for temporal differences in lizard community composition and abundance. To meet assumptions of statistical tests, proportion data were arcsine-square root transformed prior to analysis (Zar 1984). Because of low sample size in all habitats, the data did not meet all the assumptions of normality for parametric statistical tests. Both parametric and nonparametric analyses were used to test for statistically significant differences among sites (α=0.05), and results are reported for both methods. All statistical analyses were performed with Systat (version 5.0, Evanston, IL).

Results

Ten species representing three families and four genera were recorded in Guánica forest (Table 3). The distributions of many species were rather patchy, even within a continuous forest. The cosmopolitan species were: *Anolis cristatellus, Ameiva exsul, Ameiva wetmorei*, and *S. nicholsi*, which were found at all sites. *Anolis cooki* was found only at the coastal site, although a single individual was found in a ravine in close proximity to the coast.

Lizard communities at all sites were consistently dominated by two species, *Anolis cristatellus* and *S. nicholsi* (Fig. 2), which comprised at least 75% of the lizard community at all four sites. Differences in proportional community similarity (Table 4) reflect differential community composition relative to available microhabitat characteristics (e.g., slope, aspect, litter layer). The dominance of *Anolis cristatellus* and *S. nicholsi* at each site resulted in relatively low diversity (Shannon Index, H') and evenness (H'/H'_{max}) estimates (Table 5). The number of lizard species did not differ significantly among the four habitat types (sites) (Kruskal-Wallis ANOVA, P = 0.454). Additionally, absolute abundance of lizards did not differ significantly in the coastal, central, and northern Guánica forest sites between 1997 and 1998 (paired *t* test, P = 0.908).

Absolute abundance differed significantly among sites within Guánica forest (Tables 6 and 7). Three species also showed statistically significant associations with the sites. *Anolis cooki* was significantly more abundant at the coastal site, while *Anolis cristatellus* was more abundant in the other three sites as compared to the coastal site.

Table 3. Lizard species present in study sites within Guánica forest.

Species	Coastal	Central	North	Ravines	Total
Anolis cristatellus	X	X	X	X	X
Anolis cooki	X			X	X
Anolis stratulus		X	X	X	X
Anolis pulchellus	X	X	X		X
Anolis poncensis	X	X			X
Ameiva exsul	X	X	X	X	X
Ameiva wetmorei	X	X	X	X	X
Sphaerodactylus nicholsi	X	X	X	X	X
Sphaerodactylus roosevelti	X	X	X		X
Phyllodactylus wirshingi	X		X	X	X
Species richness	9	8	8	7	10

Sphaerodactylus nicholsi was more abundant in ravines than any other site.

Percent rock cover and litter depth differed significantly among sites (ANOVA, $P<0.001$). Plots sampled in the central site had significantly lower percentage rock cover and a deeper litter layer than the other 3 sites (Figs. 3 and 4, respectively). The density of *S. nicholsi* was significantly correlated with litter depth (Spearman Rank correlation, $r_s=0.227$, df=90, $P<0.05$). There were no significant differences in the composition of the lizard community or abundances of any individual species with respect to aspect. Although aspect may be very important in structuring plant communities in the dry forest (Ramjohn *et al.* 1998), it did not appear to play an important role in structuring lizard communities in this region.

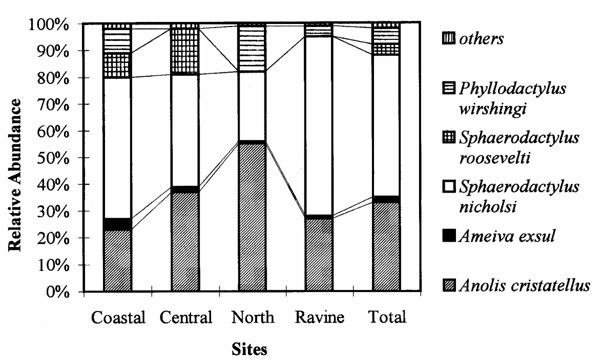

Fig. 2. Relative abundance of lizard species in Guánica forest. Species composition was not significantly different among sites (Kruskal-Wallis ANOVA, P=0.454).

Discussion

Guánica forest is the most extensive tract of dry forest in Puerto Rico, and it supports the richest and most complete native dry forest lizard community on the island (Genet 1999). This large and continuous forest offers a wide variety of habitat types that accommodate many species' ecological preferences. Of the 13 species that have been recorded in the dry zone of southwestern Puerto Rico (Table 1, Rivero 1978; Schwartz & Henderson 1991), 10 were found within Guánica forest in this study.

The three species that were absent from Guánica forest were *Sphaerodactylus macrolepis, Hemidactylus brooki*, and *Mabuya mabouya. Sphaerodactylus macrolepis* has been reported to occur in the more humid ravines within the northern boundaries of Guánica forest (M. Canals Mora, pers. comm.), but was not encountered during this study, perhaps as a result of its relative rarity and patchy distribution in the most arid parts of the island (Rivero 1978; Schwartz & Henderson 1991). *Hemidactylus brooki* is primarily edificarian, and although it is rarely encountered in natural forested situations, this species is very abundant in

Table 4. Proportional similarity of sites within Guánica forest.

Site	Coastal	Central	North
Central	0.75		
North	0.59	0.65	
Ravines	0.81	0.71	0.58

Table 5. Relative abundances of lizard species, community diversity, and community evenness.

Species	Coastal	Central	North	Ravines	Total
Anolis cristatellus	0.23	0.38	0.55	0.27	0.33
Anolis cooki	0.02	0	0	<0.01	<0.01
Anolis stratulus	0	0.01	0.01	0.01	0.01
Anolis pulchellus	<0.01	<0.01	<0.01	0	<0.01
Anolis poncensis	<0.01	<0.01	0	0	<0.01
Ameiva exsul	0.04	0.02	0.01	0.01	0.02
Ameiva wetmorei	0.01	<0.01	<0.01	<0.01	<0.01
Sphaerodactylus nicholsi	0.53	0.42	0.26	0.67	0.53
Sphaerodactylus roosevelti	0.09	0.17	<0.01	0	0.05
Phyllodactylus wirshingi	0.09	0	0.18	0.04	0.07
Diversity (H')	0.59	0.48	0.45	0.35	0.49
Evenness (J')	0.62	0.57	0.53	0.45	0.49

and around buildings, even in the Guánica area (Schwartz & Henderson 1991, pers. obs.). *Mabuya mabouya* is also extremely rare in Puerto Rico, with fewer than 15 specimens collected from the island (Rivero 1978).

Anolis cooki abundance was greatest at the coastal site (Table 5). One individual was also recorded from one of the ravines sampled in close proximity to the coast. This species was conspicuously absent from inland and upland locations. Previous studies have indicated that *Anolis cooki* is restricted to a limited number of discontinuous coastal scrub habitats within 1 km of the coast in southwestern Puerto Rico (Jenssen 1990; Marcellini *et al.* 1985). Over the past two decades, field studies have documented disappearing populations, reductions in the extent of its previous distribution, and microhabitat invasions by *Anolis cristatellus* where the two species were previously allopatric (Jenssen *et al.* 1984; Marcellini *et al.* 1985; Ortiz 1990). *Anolis cooki* is of special concern for local conservation officials, who take its abundance and distribution into consideration in current management strategies and development planning (M. Canals Mora, pers. comm.).

Table 6. Variables that differed significantly among sites in Guánica Forest, Kruskal-Wallis ANOVA.

Variable	P value
Anolis cristatellus abundance	0.003
Anolis cooki abundance	0.013
Sphaerodactylus nicholsi abundance	0.018
Absolute transect abundance (#*Anolis* and *Ameiva* per transect)	0.005
Absolute plot abundance (#geckos per plot)	0.04

Although *Anolis cooki* was present in the coastal regions of Guánica forest, it was by no means abundant. Ortiz (1990) reported that *Anolis cooki* was locally abundant where present, but low population densities reported here could be indicative of increased competitive pressure from *Anolis cristatellus*. Williams (1972) was the first to suggest that *Anolis cooki* was potentially threatened by extinction, and evidence of competitive interference and displacement into less desirable habitats (both attributable to the more abundant and widespread *Anolis cristatellus*) indicates that *Anolis cooki* is under intense ecological pressure and has an uncertain future (Jenssen 1990; Jenssen *et al.* 1984; Marcellini *et al.* 1985; Ortiz & Jenssen 1982).

Another anoline lizard, *Anolis poncensis*, is restricted to the arid regions of southwestern Puerto Rico (Schwartz & Henderson 1991). In this study, it occurred only at the coastal site in Guánica forest, but was rarely encountered, if at all, during quantitative transect sampling. This species is a grass-bush ecomorph (*sensu* Williams 1983), and shares much of its habitat with *Anolis pulchellus*, a much more widely distributed species that is often found at extremely high population densities in grassy habitats (up to 20,000 individuals ha^{-1}, Gorman & Harwood 1977). Where sympatric, *Anolis poncensis* often occupies bushes and fenceposts

Table 7. Densities of lizards in Guánica forest. One-way ANOVA was used to test for differences among sites. Numbers represent mean densities (individuals ha^{-1}) with their standard errors, and values within a row with matching superscripts differ significantly from one another (Tukey's HSD, $P<0.05$). n = total number of individuals per site, *species that were recorded at a site but not during quantitative sampling, precluding density estimation.

Species	Coastal		Central		North		Ravines	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Anolis cristatellus	275[ab]	63	461[c]	119	651[a]	64	877[bc]	15
	n=68		n=114		n=161		n=217	
Anolis cooki	24[abc]	9	0[a]	0	0[b]	0	4[c]	4
	n=6		n=0		n=0		n=1	
Anolis stratulus	0	0	8	5	8	8	32	23
	n=0		n=2		n=2		n=8	
Anolis pulchellus	*		*		*		0	0
							n=0	
Anolis poncensis	*		*		0		0	
					n=0		n=0	
Ameiva exsul	42	14	24	11	6	4	32	24
	n=11		n=6		n=2		n=8	
Ameiva wetmorei	9	3	6	4	4	3	2	2
	n=2		n=2		n=1		n=2	
Sphaerodactylus nicholsi	625[a]	343	521[b]	219	313[c]	152	2222[abc]	852
	n=6		n=5		n=3		n=16	
Sphaerodactylus roosevelti	104	104	208	208	*		0	0
	n=1		n=2				n=0	
Phyllodactylus wirshingi	104	104	0	0	208	136	139	139
	n=1		n=0		n=2		n=1	

while *Anolis pulchellus* seems to prefer the more exposed grassy areas (Rivero 1978). To our knowledge, the potential for competitive interference and displacement between *Anolis poncensis* and *Anolis pulchellus* has not been assessed, although these two species may represent a dynamic situation similar to that discussed above for *Anolis cooki* and *Anolis cristatellus*.

The four sites represented different habitat types within a contiguous forest, and habitat variables differed significantly among these sites. The central site in Guánica forest had significantly less rock and deeper leaf litter as compared to the other three sites. Geckos would be expected to respond to variations in substrate habitat, as they are found primarily in and among substrate debris in all habitat types in the dry forest region (Rivero 1978). *Sphaerodactylus nicholsi* abundance showed a significant positive correlation with leaf litter depth for the upland sites in our study. However, *S. nicholsi* was much more abundant in ravines than at the central site where the litter layer was deepest. Throughout its range *S. nicholsi* prefers dry habitats and is typically absent from mesic sites (Thomas & Schwartz 1966). In contrast, our results indicated that the mesic semi-evergreen ravines within the dry forest supported a high density of *S. nicholsi* compared to more xeric deciduous forest and coastal scrub. The distribution and abundance of *S. nicholsi* in Guánica forest may reflect the abundance and stability of prey populations that probably occur in the more mesic ravines. Although average litter depth was not greatest in the ravines, we observed areas in the ravines with deep litter accumulation; pulses of litter input from storm events import litter and result in thick litter mats, especially where there are rocks and downed trees to block water flow. It is possible that these areas were not included in our random plot selection. *Sphaerodactylus roosevelti* and *P. wirshingi* abundance would also be expected to vary with substrate characteristics, but their low occurrence in this study precluded the detection of any significant patterns.

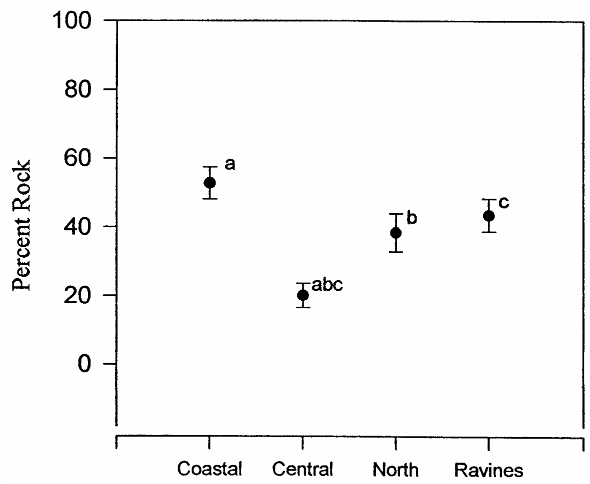

Fig. 3. Differences among sites in percentage rock cover in 2 m x 2 m subplots (mean ± std. error). Points with matching letters indicate significant pairwise difference (Tukey's HSD, P<0.05).

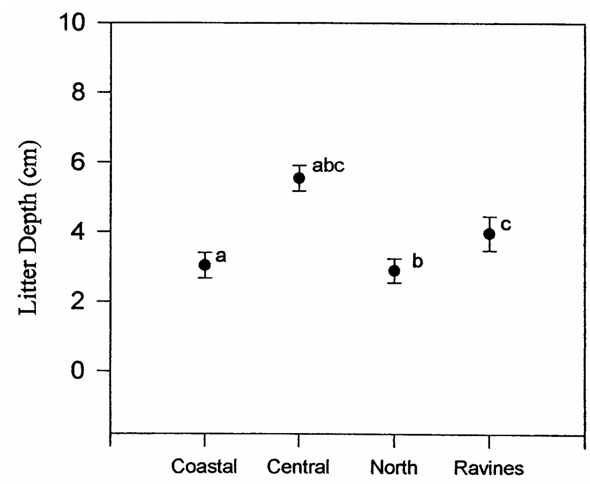

Fig. 4. Differences among sites in litter depth in 2 m x 2 m subplots (mean ± std. error). Points with matching letters indicate significant pairwise differences (Tukey's HSD, P<0.05).

Anolis cristatellus abundance also differed significantly among the four sites. This species was least abundant at the coastal site, where it is competing and partitioning the habitat with the other trunk-ground ecomorph, *Anolis cooki*. Since anoline lizards are largely arboreal, the number and distribution of trees present in the habitat influence the density of individuals. The four sites differ in the distribution of trees and tree species composition (Lugo *et al.* 1978), perhaps leading to differences in *Anolis cristatellus* density. The ravines contain larger mature trees and more abundant vines and lianas than the surrounding dry forest (Farnsworth 1993), which provide perches for these arboreal lizards. Within the reference site, semi-evergreen forest has higher basal area as compared to deciduous and scrub forest types, but stem density is greatest in deciduous forest (Castilleja 1991; Lugo *et al.* 1978; Ramjohn *et al.* 1998).

The total number of lizards encountered during quantitative sampling varied greatly among species. While patterns potentially exist to explain distribution and abundance of the less common lizard species within Guánica forest, the small populations and patchy distribution of these species did not allow determination of any noticeable trends. Other investigators have used transect surveys to efficiently and accurately estimate lizard population densities (Rand 1964; Reagan 1992; Schoener & Schoener 1971a, b). Juvenile anoles that have not yet established their territories may be more mobile and introduce error into this method, but Andrews & Rand (1983) suggested that the mean distance between captures of juvenile *Anolis limifrons* on Barro Colorado Island in Panama was 2.9 m, a distance contained within our circular transect sample plot. Altering the survey methods would also lead to more accurate density estimates for certain species. Some species (i.e., *Anolis stratulus*) are present in the forest canopy in numbers greater than can be accurately detected from ground-level observations, and vertical transect methods yield dramatically higher density estimates than ground transects (Reagan 1992, 1996). The relative abundance and density estimates reported here for *Anolis stratulus* are likely to be underestimates for these reasons.

It is important to asses the ecological communities of reserves to determine their adequacy for conservation of these communities. It is clear from other studies of lizard communities in arid regions that the amount and heterogeneity of habitat types are important to support diverse lizard communities (e.g., the western Australian Wheatbelt; Kitchener *et al.* 1980). Habitat area and vegetation associations are important factors for lizard community structure and composition (Kitchener & How 1982; Kitchener *et al.* 1980); the integrity of intact forests and their natural vegetation communities need to be preserved for their resident fauna (Lenart *et al.* 1997). Lizard communities are threatened by habitat alteration and predation (especially by introduced predators) not only in the dry forest region of Puerto Rico, but throughout the Caribbean region (Henderson 1992). Studies of lizard communities in intact, relatively undisturbed large forests is necessary for the evaluation of the effects of widespread habitat alteration and predation in the Caribbean.

In conclusion, the lizard community of Guánica forest is comprised of 10 species, some of which are differentially distributed throughout the four different forest habitat types sampled in this study. This forest offers excellent habitat for dry forest lizards, and this study provides baseline conditions against which data from other areas can be compared. Remaining dry forest habitat in southwestern Puerto Rico as well as other regions of subtropical and tropical dry forest exists as fragments of varying size, degree of isolation, and vegetation type. It is important to determine the impact of large-scale habitat fragmentation on the distribution and abundance of dry forest lizards in order to assess the status and conservation potential of both the species and the forest fragments in the dry forest life zone of southwestern Puerto Rico.

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