



Lizard diversity and agricultural disturbance in a Caribbean forest landscape

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Abstract. Understanding the impact of agriculture on biodiversity is critical for effective conservation management. Our goal was to determine the impact of agricultural disturbance on the lizard fauna of Los Haitises National Park and the surrounding region in the Dominican Republic. This region has a history of extensive agricultural disturbance followed by abrupt abandonment. Abundance and diversity were surveyed in six habitats: relatively undisturbed hilltop (*mogote*), four habitats disturbed by agriculture (pasture, oil palm plantation, cacao plantation, conuco or home garden), and one forested habitat. Three of these habitats (pasture, cacao plantation, conuco) were also examined at different stages of activity or abandonment. Glue-trap grids were used to sample each habitat. In general, species richness was lower in more heavily or recently disturbed habitats. Richness was lowest in active agricultural habitats where only 54% of the region's lizard species were detected. Notably, agricultural systems differed considerably in their ability to support a diverse lizard assemblage. Abandoned agricultural habitats had slightly higher richness than their active counterparts, but still contained only 69% of the region's species. By contrast, nearly every native species, including several never observed in agriculturally disturbed habitats, were detected on the undisturbed hilltops (*mogotes*). These *mogotes* may have served as refuges for species that could not tolerate disturbance when the region was being heavily exploited for agriculture. Overall, our results suggest that the continued protection of the park, and its *mogotes* in particular, will be required to maintain the region's lizard diversity.

Key words: agroecology, *Anolis*, biodiversity, Dominican Republic, Los Haitises National Park

Introduction

Humans have directly disturbed most habitats (Western and Pearl 1989) resulting in reduced biodiversity and other profound ecological changes (Ehrlich 1988; Lugo 1988; Estrada et al. 1993, 1998; Power 1996). Ideally, the preservation of biodiversity and ecosystem functioning would occur in undisturbed habitats protected from human exploitation. However, the most practical conservation tactic in many cases may be for humans to take an active role in managing ecosystems. Such management aims to allow for some level of human use while maintaining maximal biodiversity (Ocana et al. 1988; Janzen 1998). However, in order to avoid the criticisms of previous

management attempts (e.g. Bawa and Seidler 1998) future strategies will require detailed a priori knowledge about the ecological effects of human disturbance.

One way to acquire this knowledge is by surveying biodiversity in landscapes consisting of undisturbed habitat and a range of disturbed habitats. Although such surveys often lack an experimental aspect, they are nonetheless capable of providing useful comparative information about the ecological effects of specific types of disturbances. This comparative information may be valuable in the identification of human practices that have particularly strong effects on biodiversity as well as species and habitats that are most susceptible to disturbance. Ultimately, comparative surveys in disturbed landscapes may be useful in determining how much native biodiversity can be maintained in disturbed habitats and may facilitate attempts to tailor human practices to sustain maximal biodiversity.

Previous studies of disturbed landscapes suggest variable ecological effects depending on the form and degree of disturbance as well as the taxa being surveyed. However, most studies with animals indicate that disturbance reduces diversity (Janzen 1973a,b; Room 1975; Heinen 1992; Estrada et al. 1993, 1998; Roth et al. 1994; Blair 1996; Greenberg 1996; Power 1996; Burel et al. 1998). Despite decreases in diversity, animal abundance often increases following disturbance due to a superabundance of common or introduced species while certain rare native species are restricted to undisturbed habitats (Heinen 1992; Estrada et al. 1993; Power 1996; Blair 1996).

Agriculture is one of the most common forms of human disturbance and comes in many forms with a variety of ecological effects. However, the ecological effects of most forms of agriculture have yet to be studied in detail. The purpose of the present study was to examine the effects of various forms of tropical agriculture on lizard diversity in and around Los Haitises National Park, Dominican Republic. A number of factors make lizards particularly appropriate for a study of diversity in the Los Haitises region: (1) They are the most abundant vertebrates in the West Indies and are central food web components (Reagan 1996); (2) many of the park's lizards are diurnal and relatively easy to sample; (3) lizards are systematically well known and readily identifiable in the field; (4) previous research has indicated that West Indian lizard species richness may be affected by human disturbance (Lenart et al. 1997); and (5) the microhabitat preferences of many of the region's lizards are well known (Williams 1983; Losos and deQueiroz 1997).

Although Los Haitises National Park was established in 1976, nearly all of its valleys were used for agriculture until 1993, when the Dominican government removed the park's residents and began to protect it from further exploitation. The abrupt end to agricultural practices left the park as a patchwork of habitats ranging from clear-cut pasture to the relatively undisturbed tops of the area's haystack hills or *mogotes*.

The park's history provided a unique opportunity to examine the effects of human land use on biodiversity including ecological recovery following abandonment.

The present study was initiated 4 years after active agriculture ended in the park. Consequently, we examined several active agricultural plots located just outside the park's boundaries for comparative purposes. Our goal was to answer the following questions: (1) Does the park maintain higher lizard diversity than the surrounding active agricultural habitats? (2) What portion of the lizard community can survive in agricultural habitats? (3) How have specific forms of agriculture affected lizard diversity and subsequent faunal recovery? Our results should provide insight as to whether those land use patterns preserving some semblance of structural complexity of forest ecosystems are important to maintaining lizard diversity within an agriculturally dominated landscape.

Methods

Study site

Los Haitises National Park is located on the southwest corner of Samana Bay in the Dominican Republic. The karstic haystack hills (*mogotes*) which characterize the park cover less than 10% of the Dominican Republic's land area (Zanoni et al. 1990). The vegetation of Los Haitises is classified as subtropical broadleaf forest with some differences in vegetational composition between the narrow valleys and *mogotes* (Zanoni et al. 1990). The average annual rainfall of the Los Haitises region is approximately 2000 mm (Zanoni et al. 1990).

In the summer of 1996, 24 study plots were established in three regions in the northeastern section of Los Haitises National Park, near the former communities of Caño Hondo, Los Naranjos, and Trepada Alta. Each plot was classified as one of six habitat types on the basis of vegetational structure and accounts from park guards who once lived and farmed in the park. The size of the plots was variable and depended primarily on the size of the valley available for agriculture.

Habitats examined were: abandoned pasture (4 plots), young conuco (7 plots), old conuco (5 plots), abandoned cacao plantation (2 plots), remnant forest (2 plots), and *mogote* top (4 plots). Abandoned pastures were once clear cut and were used for grazing livestock until 1993; today they are characterized by dense ferns, small trees, and shrubs. Home gardens, or conucos, were mixed cropping systems containing a diversity of introduced species such as banana, coconut, beans, pineapple, and citrus trees. Young conucos had been abandoned for less than 5 years at the time the study was initiated, while old conucos had been abandoned for 5–10 years (Los Haitises Park Guards, pers. comm.). Abandoned cacao plantations, which contained mature cacao trees and scattered large shade trees, had reportedly been abandoned for as many as 80 years (Los Haitises Park Guards, pers. comm.). The remnant forest patches were rare habitats that did not contain crop plants but some large trees had been removed for timber. *Mogote*

tops were inconvenient for agriculture and represented the only habitat in the park that remained largely undisturbed. Not all habitat types occur in all regions, so a completely balanced sampling protocol was not possible.

In addition to the habitats inside the park, three active agricultural habitats located on the periphery of the park were also examined: active pasture (3 sites), active oil palm plantation (3 sites), and active cacao plantation (3 sites). Active pastures were characterized by low growing grass, sparse trees and shrubs, and abundant livestock. Oil palm plantations, a form of agriculture never practiced in the park, were large commercial operations that contained little plant life except for large uniformly spaced African oil palm trees (*Elaeis* sp.). Active cacao plantations contained cacao trees (*Theobroma cacao*) as well as large shade trees left by farmers when forests were cleared in order to shade the cacao.

Sampling protocol

Our sampling protocol involved 10×10 m trapping grids consisting of 20 Victor™ mouse glue traps in 30 of the 33 sites. The use of glue traps for sampling lizards is a relatively new technique (Bauer and Sadler 1992; Rodda et al. 1993; Whiting 1998; Vargas et al. 2000) and to our knowledge this study represents the first report of their use in the West Indies. The traps were capable of capturing all lizard species known to occur in the Los Haitises region.

Our glue trap sampling protocol was developed between 29 December 1996–17 January 1997, and all data reported here were collected between 11 July–3 August 1997 (wet season) and 29 December 1997–17 January 1998 (dry season). In each plot, four microhabitats were sampled using five traps in each (4 microhabitats \times 5 replicate traps = 20 traps per grid). Microhabitats sampled were: (1) open ground, at least 1 m away from the nearest tree; (2) ground at base of tree; (3) tree trunk or branch, 1 m above the ground; and (4) tree trunk or branch, 2 m above the ground.

Trapping grids required a minimum of fifteen trees as no more than one trap was associated with each individual tree. This fifteen tree minimum necessitated the use of non-randomly selected grids in habitats where trees were scarce (i.e. abandoned pastures). In the case of active pastures, which were almost completely devoid of trees, all twenty traps were placed on the ground.

Traps were checked every 24 h for the duration of the 120 h trapping cycle carried out in each plot. Wet and damaged traps were replaced when necessary. Lizards were released from the traps by loosening the glue around their limbs with vegetable oil and one toe-nail was clipped so that the lizard could be recognized if recaptured. Recaptured lizards were not counted a second time. Additional statistics associated with our sticky trap sampling protocol (i.e. mortality in traps, rates of capture, etc.) can be found in Glor et al. (2000).

Data analysis

Diversity incorporates information about both species richness and evenness and its measure has been the subject of considerable controversy (Magurran 1988; Hengeveld 1996). We analyzed richness alone using rarefaction and richness and evenness together using two diversity indices. In order to compensate for differences in sample size we used rarefaction curves for species richness generated by the hypergeometric formula and its associated 95% confidence limits (Gotelli and Graves 1996). The diversity indices calculated were Hurlbert's PIE (Probability of Interspecific Encounter) and the log series index (α). Formulas for calculating these statistics and discussions of their strengths and weaknesses are discussed in greater detail elsewhere (Magurran 1988; Hayak and Buzaz 1994; Gotelli and Graves 1996).

Results

Three families of lizards were sampled, each represented by a single genus (Table 1). Five species of the genus *Anolis* (Iguanidae) dominated the lizard fauna, accounting for 89.7% of the total lizards sampled (Table 1). Three species of the genus *Celestus* (Anguidae) were sampled in small numbers. Dwarf geckos (*Sphaerodactylus*, Gekkonidae) were rarely sampled, but were a species-rich group represented by five taxa.

Species richness was higher inside the park than in the surrounding active agricultural sites (Figure 1, Table 2). We sampled over 90% of the lizard species native to the region in the park, but only 54% outside the park. Furthermore, all habitat types in the park had higher richness than each of the habitats sampled outside the park. Raw richness was highest on *mogote* tops, which had three more species than any other park habitat and six more species than any active agricultural habitat. This was due, in part, to the presence of three species of dwarf geckos (*Sphaerodactylus*) found only on *mogotes*. Raw richness was also higher in old conuco vs. young conuco, abandoned cacao vs. active cacao, and abandoned pasture vs. active pasture (Figure 1, Table 2). In each case, these results indicate a slight increase in richness following abandonment.

Rarefaction curves were fitted for all habitats except the active pasture where the number of individuals captured was too small (Figure 2). Most curves appear to approach an asymptote fairly quickly. This indicates that even samples rarefied to 46 individuals (the fewest individuals of any sample except active pasture) provide a reasonable estimate of the actual richness relationships of the habitat types fairly accurately. Samples rarefied to 46 individuals indicate that richness was highest on the *mogote* followed by abandoned cacao, remnant forest, old conuco, abandoned pasture, active cacao, oil palm, and young conuco. Active agricultural sites generally had lower richness than park sites. However, there was extensive overlap of the

Table 1. Summary of lizards captured in glue traps. For each species, the first number represents the number of individuals sampled, while the number in parentheses represents the relative contribution of that species to the column.

Species	Active sites										Grand totals	
	Active pasture	Oil palm	Active cacao	Active sites totals	Aband. pasture	Young conuco	Old conuco	Aband. cacao	Forest	Mogote		Park totals
Iguanidae												
<i>Anolis baleatus</i>	-	-	2 (0.9)	2 (0.6)	2 (1.7)	1 (0.5)	5 (3.2)	1 (2.2)	3 (3.6)	5 (2.9)	16 (2.1)	19 (1.7)
<i>A. chlorocyanus</i>	-	4 (4.3)	10 (4.3)	14 (4.3)	16 (13.3)	21 (9.8)	10 (6.5)	1 (2.2)	4 (7.3)	11 (6.5)	63 (8.3)	77 (7.1)
<i>A. cybates</i>	2 (67)	56 (59.6)	68 (29.3)	126 (38.3)	2 (1.7)	4 (1.9)	1 (0.6)	-	-	22 (12.9)	29 (3.8)	155 (14.2)
<i>A. distichus</i>	1 (33)	19 (20.2)	145 (62.5)	165 (50.2)	82 (68.3)	163 (75.8)	110 (71)	32 (69.6)	38 (69)	91 (53.5)	516 (67.8)	681 (62.5)
<i>A. semilineatus</i>	-	-	-	-	12 (10)	21 (9.8)	6 (3.9)	1 (2.2)	5 (9)	13 (7.6)	58 (7.6)	58 (5.3)
Anguidae												
<i>Celestus costatus</i>	-	2 (2.1)	-	2 (0.6)	-	-	-	-	-	-	-	2 (0.2)
<i>C. stenurus</i>	-	13 (13.8)	-	13 (4)	6 (5)	4 (1.9)	17 (11)	8 (17.4)	5 (9)	5 (2.9)	45 (5.9)	58 (5.3)
<i>C. sepsoides</i>	-	-	-	-	-	1 (0.5)	1 (0.6)	1 (2.2)	1 (1.8)	-	4 (0.5)	4 (0.4)
Gekkonidae												
<i>Sphaerodactylus cochranae</i>	-	-	-	-	-	-	-	-	-	8 (4.7)	8 (1.1)	8 (0.7)
<i>S. clenchi</i>	-	-	-	-	-	-	-	-	-	1 (0.6)	1 (0.1)	1 (0.1)
<i>S. darlingtoni</i>	-	-	-	-	-	-	-	-	-	7 (4.1)	7 (0.9)	7 (0.6)
<i>S. difficilis</i>	-	-	7 (3)	7 (2)	-	-	5 (3.2)	1 (2.2)	-	6 (3.5)	12 (1.6)	19 (1.7)
<i>S. samanensis</i>	-	-	-	-	-	-	-	1 (2.2)	-	1 (0.6)	2 (0.1)	2 (0.02)
Total individuals	3	94	232	329	120	215	155	46	55	170	761	1090
Total species	2	5	5	7	6	7	8	8	6	11	12	13

Values in parentheses are in percentage.

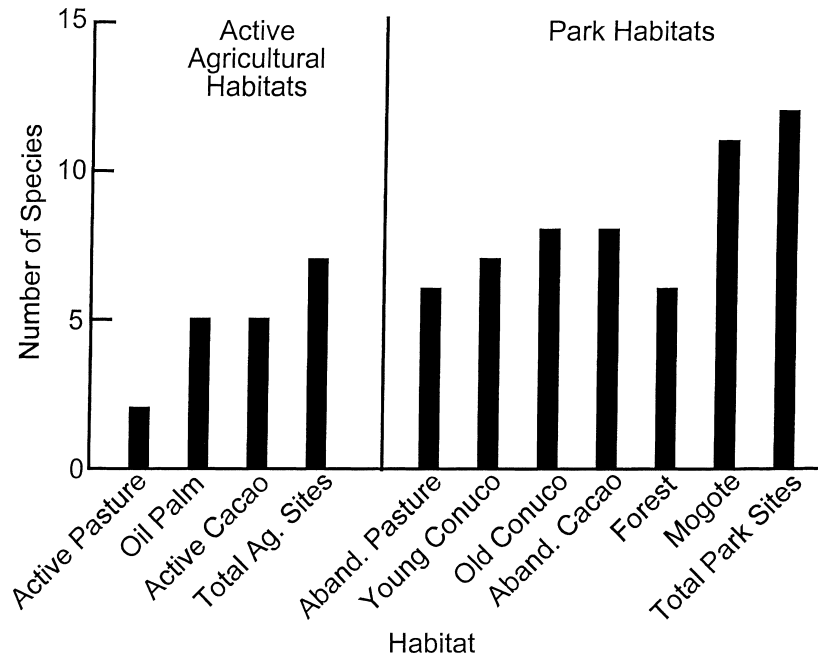


Figure 1. Raw species richness of habitats sampled for both trapping and transect samples.

95% confidence intervals at 46 individuals (Figure 2b). Interestingly, *mogotes* had significantly higher richness than any other habitat at 46 individuals (Figure 2b).

Although samples rarefied to 46 individuals appear to provide reasonable estimates, it is clear that some habitats would change relative to one another if the curves were compared at more individuals. For example, at 46 individuals, richness of young

Table 2. Summary of statistics from glue trap sampling data. Several diversity could not be calculated for active pasture because of the low sample size.

Habitat	Plots examined	Individuals	Raw richness	Richness ^a	Hurlbert's PIE	α Diversity index
Active sites						
Active pasture	3	3	2	—	—	—
Oil palm plantation	3	94	5	4.71	0.59	0.87
Active cacao plantation	3	232	5	4.92	0.57	1.38
Park sites						
Abandoned pasture	4	120	6	4.95	0.51	0.85
Young conuco	7	215	7	4.63	0.41	1.16
Old conuco	5	155	8	5.39	0.48	1.45
Abandoned cacao	2	46	8	7	0.49	1.33
Forest	2	55	6	5.81	0.51	1.09
Mogote	4	170	11	8.77	0.68	1.73

^a Based on random samples rarefied to 46 individuals.

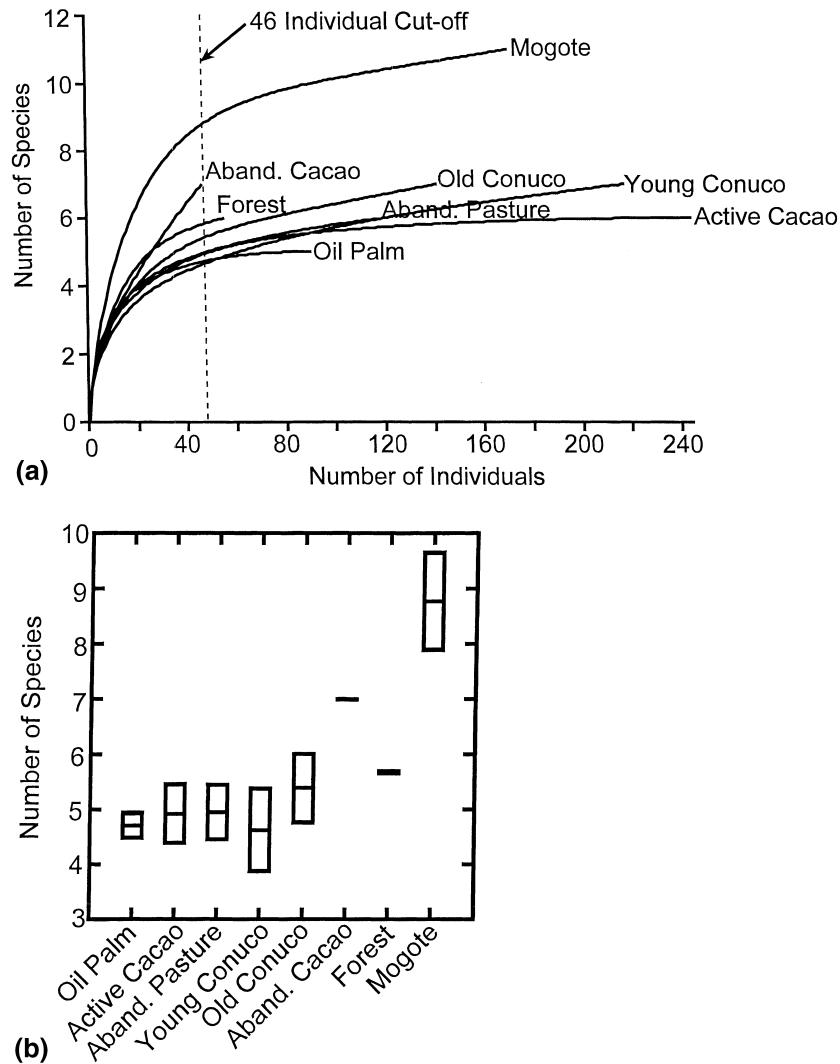


Figure 2. (a) Rarefaction curves constructed using the hypergeometric formula, (b) 95% confidence limits for rarefaction curves at 46 individuals.

conuco is lower than active cacao, however conuco surpasses cacao if the curves are compared for more than 90 individuals.

Hurlbert's PIE indicates that diversity is highest on *mogotes* and lowest in young conucos (Table 2). PIE was higher in oil palm and cacao plantations, where two lizard species were co-dominant, than in all park habitats except for *mogotes*. The log series index also found the highest diversity on *mogotes* (Table 2). Abandoned pastures and oil palm plantations had the lowest diversity values calculated by the log series index (Table 2). However, it is important to remember that diversity was actually lowest in

active pastures, but was so low in these plots that diversity indices could not even be calculated.

Discussion

All forms of agriculture practiced in the Los Haitises region appear to have had a strong negative impact on lizard diversity. Species richness was particularly low in the most heavily or most recently disturbed habitats. Species richness in active agricultural habitats was always lower than in abandoned agricultural habitats (Figure 1, Tables 1 and 2). Although this finding suggests a slight increase in richness following abandonment, even abandoned habitats did not demonstrate richness comparable to that of *mogote* tops. *Mogotes* contained nearly all of the species found in disturbed habitats as well as three species of dwarf geckos (*Sphaerodactylus*) found nowhere else. Overall, these results suggest a considerable drop in diversity following disturbance with the potential for modest short-term faunal recovery following abandonment.

Although experimental work will be required to confirm these results, our finding of decreased diversity with increased agricultural disturbance is in agreement with the results from a number of other studies in disturbed landscapes (Room 1975; Estrada et al. 1993, 1998; Blair 1996; Lenart et al. 1997; Burel et al. 1998). In a previous study with Dominican anoles, Lenart et al. (1997) reported considerably higher diversity in structurally complex forest patches and coffee plantations relative to neighboring clear-cuts. Surveys in an agriculturally disturbed landscape in Mexico with a range of habitats similar to those of the Los Haitises region generated results similar to ours (Estrada et al. 1993, 1998). Estrada et al. (1993, 1998) found that dung beetle, carrion beetle, and bat diversity are highest in forest patches, lower in shaded plantations (cacao, coffee, and mixed) and lower still in open pasture habitats.

Several hypotheses have been put forward to explain the correlation between low diversity and disturbance including: (1) decreased structural complexity and microhabitat availability in disturbed habitats; (2) shifts in microclimatic conditions resulting from disturbance; (3) reduced food resources in disturbed areas; (4) time lags in recolonization of native species into severely disturbed habitats; and (5) indirect effects of disturbance acting through interactions between species (Janzen 1973b; Heinen 1992; Estrada et al. 1993; Greenberg et al. 1996; Blair 1996; Perfecto et al. 1997; Burel et al. 1998). Clearly, these hypotheses are not mutually exclusive and further study may prove that all of these factors are acting in concert to generate observed patterns of lizard diversity in Los Haitises.

However, the results of this study, together with the known natural history of the region's lizards, suggest that microhabitat availability is a major factor in at least two cases. In each of these cases, the elimination of a particular microhabitat appears to be correlated with the absence of the lizard species that specializes on that microhabitat.

First of all, the grass-bush anole (*A. semilineatus*), which inhabits the forest understory (Williams 1983), was never detected in active agricultural habitats. In these habitats, the understory is almost completely absent due to active weeding, the application of herbicides, and intense human activity in general. In the second case, the rare Cochran's dwarf gecko (*S. cochranae*) was present only on *mogotes*, where it was encountered almost exclusively in and around bromeliads. Bromeliads were abundant on *mogotes*, but were noticeably absent from agriculturally disturbed habitats.

Ecological impact of agricultural practices

Although all forms of agriculture appear to generally reduce biodiversity, the degree of disturbance was highly variable between different agricultural practices. Not surprisingly, lizard communities were most depauperate in the active pastures (Table 2, Figure 1). The slight faunal recovery that was evident in the abandoned pastures (Table 2) is likely a reflection of rapid floral recovery; less than five years after abandonment, pastures in the park were already filled with dense shrubs and small trees (Power et al. 1997), providing ample perches, cover, and shade for certain lizard colonists.

Another form of agriculture associated with clear-cutting, the oil palm plantation, provided suitable habitat for less than 40% of the region's lizards. Though oil palm trees form an artificial forest habitat with considerable shade cover, the oil palm monoculture clearly lacks the perch availability and understory microhabitat of a natural forest. Previous studies have reported lower ant diversity in oil palm relative to native forest (Room 1975).

Unlike pastures and oil palm plantations, cacao plantations were never clear-cut and have maintained some semblance of typical forest structure. Though previous studies have indicated relatively high diversity in cacao plantations compared to other agricultural habitats (Room 1975; Heinen 1992; Estrada et al. 1993, 1998), our results indicate similar species richness in cacao and oil palm plantations (Table 2). However, the species composition of the two was drastically different (Table 1). Oil palm was home to one species never sampled in the native forest, *C. costatus*, while the cacao plantation was one of only four habitats from which dwarf geckos, *Sphaerodactylus*, were sampled. This suggests that farming an understory crop while leaving a part of the native canopy intact may result in the maintenance of a fauna more similar to that of native forest.

Conclusions

Human disturbance, primarily in the form of agriculture, has had profound effects on the lizard fauna of the Los Haitises region. Certain lizard species are entirely absent from agriculturally disturbed habitats, while others appear to be present only

when the appropriate microhabitat has remained intact. As a group, the dwarf geckos (*Sphaerodactylus*) appear particularly susceptible to disturbance. These geckos are of particular conservation interest since two species, *S. samanensis* and *S. cochranæ*, are endemic to the Los Haitises region (Schwartz and Henderson 1994). *Sphaerodactylus cochranæ* is known from only a handful of specimens and had not been seen for over 20 years prior to its rediscovery during the course of this study (Thomas and Schwartz 1983). It has recently been included in a list of threatened Dominican lizards (Powell et al. 2000).

Our results also suggest that *mogotes* are havens for lizard diversity. These habitats may well be serving as refuges for species that are unable to cope with disturbance. In fact, the relative inaccessibility of *mogotes* for agriculture may have played a significant role in preserving native lizard diversity prior to 1993 when the entire area now protected by the park's borders was being heavily exploited for agriculture. Clearly, the continued protection of Los Haitises National Park, and its *mogotes* in particular, will be necessary if the lizard diversity of this area is to be sustained. However, the potential for increasing the capacity of agricultural habitats to maintain a higher proportion of native biodiversity also deserves further study.

On a regional scale, our findings may be representative of broader patterns of lizard diversity in other disturbed Caribbean forests. A comparable pattern of lizard diversity is especially likely to be uncovered on other Greater Antillean islands, where similar forms of agriculture are practiced and a surprisingly similar complement of lizard microhabitat specialists has evolved independently on each island (Losos et al. 1998).

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