

## HERPETOFAUNAL DYNAMICS DURING SECONDARY SUCCESSION

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**ABSTRACT:** Concepts of vertebrate succession in terrestrial habitats are based mainly on studies of birds and mammals. To provide a broader understanding of vertebrate succession and the organization of species assemblage, we studied the development of a herpetofaunal assemblage in a reforestation project. We sampled herpetofauna monthly between February 2001 and March 2002 and between June and September 2003 in a reforested limestone valley, and compared the composition and structure of the species assemblage in this valley with three reference sites and a deforested valley in a limestone region of Puerto Rico. In the reforested valley, the increase in vegetation heterogeneity and the decrease in microclimate variability facilitated herpetofaunal succession. Species richness increased rapidly from three to eleven species in 13 mo, with predatory species colonizing the reforested valley by the end of the study. The trophic structure changed more slowly with the density of individuals of (1) arboreal species increasing with increased woody vegetation cover, and (2) predatory species increasing with increased prey density. The pattern of herpetofaunal succession can be described by an assembly rule that considers microclimate as an important controller for the development of the species assembly. We suggest that including microclimate in assembly rules can help us broaden our understanding of factors that determine vertebrate succession in terrestrial habitats.

**Key words:** Assembly rules; Community structure; Faunal succession; Habitat reforestation; Karst; Puerto Rico

FAUNAL succession, or the development of faunal assemblages, is controlled by abiotic and biotic factors that are scale and taxon dependent (Brown and Southwood, 1987; Lawton, 1987; Levin, 1992; Ricklefs, 1987; Wiens, 1989). Animals can have different perceptions of the landscape depending on the scale at which they forage and reproduce, occupy a home range, disperse to locate suitable habitats, and on physiological limitations related with climate factors along environmental gradients (Hawkins et al., 2003; Peterson et al., 1998; Rodewald and Yahner, 2001; Williams et al., 2002). In comparison with large mammals and migratory birds, small mammals, nonmigratory birds, and many reptiles and amphibians can spend much of their life in a small patch of vegetation within a landscape. The relatively small home ranges of amphibians and reptiles make them more dependent on local environmental conditions and more prone to local extinction after disturbances in comparison with birds and mammals (Blaustein et al., 1994). These differences may affect patterns of faunal succession and the organization of species assemblages.

Because herpetofauna are ectothermic, succession in assemblages of amphibians and reptiles may be more strongly affected by external environmental conditions than that of birds and mammals (Huey, 1991; Miles, 1994; Porter and Gates, 1969). Furthermore, the permeable skin of amphibians and their biphasic life cycles make them sensitive to a wide range of environmental conditions. Given that local climate can have a major influence on the distribution and abundance of species, and on the trophic structure of animal assemblages (Voigt et al., 2003), factors influencing the development of species assemblages in ectotherms can be different from factors that influence the development of species assemblages in endotherms (Duellman, 1989; Hadden and Westbrooke, 1996; Huey, 1991).

In this study, we address the following questions: (1) How does the herpetofaunal assemblage change during succession? (2) What factors influence the composition and structure of the herpetofaunal assemblage? (3) What assembly rules describe the pattern of herpetofaunal succession? To answer these questions we studied the herpetofauna in a limestone (= karst) region of Puerto Rico in the Caribbean Basin. Specifically we studied the development of a herpetofaunal

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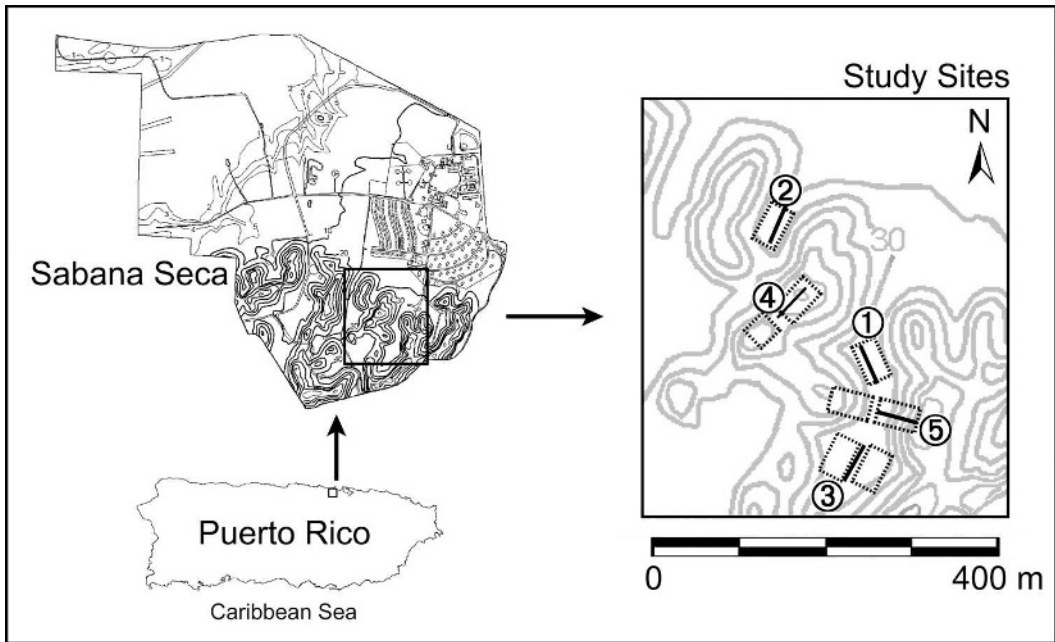


FIG. 1.—Location of the study sites in Sabana Seca, northern Puerto Rico, in the Caribbean region. Contour lines of elevation are in 10-m intervals (the 30-m mark is shown as reference). The study sites are (1) reforested valley, (2) deforested valley, (3) old valley, (4) hilltop, and (5) hillside. Vegetation plots are represented by rectangles (dash lines) in each site. Census transects are represented by straight lines inside or between vegetation plots.

assemblage in a recently reforested valley, and compared the structure of the herpetofaunal assemblage in this valley with three reference sites and a deforested valley.

#### MATERIALS AND METHODS

##### *Study Area*

We conducted this study in a karst region in Sabana Seca ( $18^{\circ}27' \text{ N}$ ,  $66^{\circ}12' \text{ W}$ ), northern Puerto Rico (Fig. 1). The region is located in the Subtropical Moist Forest life zone (Ewel and Whitmore, 1973). In this region, we worked in five sites (i.e., a reforested karst valley, three forested reference sites, and a deforested valley). The average annual rainfall and temperature is 1700 mm and  $27^{\circ}\text{C}$ , respectively (Eusse and Aide, 1999). Both rainfall and temperature are mildly seasonal with most of the rain occurring from May to November, which are also the warmest months.

In January 2000, a karst valley, previously maintained as lawn for  $>20$  yr, was reforested with 516 plants of 22 native woody species

(Appendix I) with the intent of creating habitat for the endangered Puerto Rican boa, *Epicrates inornatus*. The reforested valley is approximately 160-m long and 20-m wide. Plants were planted in a  $2 \times 3$ -m grid for a final density of  $1666 \text{ plants ha}^{-1}$ . Grasses and vines that grew beneath each plant were frequently cut during the first year after planting to reduce mortality of woody plants. Mean plant height was 0.66 m in January 2000, 1.26 m in April 2001, and 1.78 m in April 2002, for a mean growth rate of  $0.56 \text{ m yr}^{-1}$ . After 27 mo, plant survivorship was 93.6%. Although we have not measured vegetation height after April 2002, the majority of plants in the reforested valley had grown to  $>3$  m in height by April 2003 (Fig. 2). The reference forested sites consisted of an old valley, which reforested naturally 30 to 40 yr ago, and a karst hillside and a karst hilltop which have been forested for  $>65$  yr (Fig. 1). A reference deforested site (= deforested valley) consisted of a karst valley that had been maintained as lawn for  $>20$  yr.

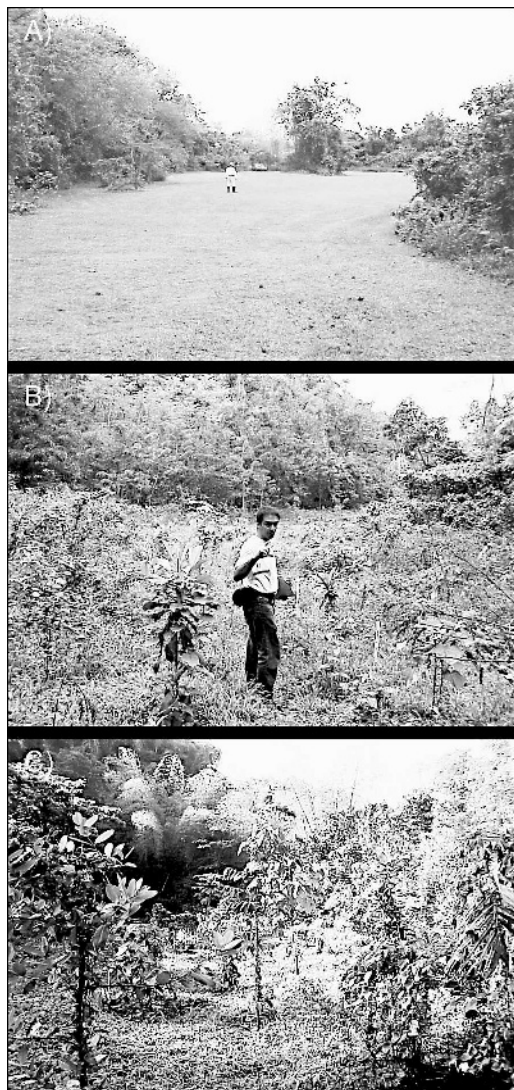


FIG. 2.—Stages of secondary (plant) succession (A) the deforested valley that represented the pre-planting conditions (~January 2000), (B) the reforested valley 15 mo after initial planting (April 2001), and (C) the reforested valley 39 mo after initial planting (April 2003).

### Species Sampling

We sampled the herpetofauna monthly in each site using the Visual Encounter Survey and Audio Strip Transect techniques (Crump and Scott, 1994; Zimmerman, 1994), during both the day and night. This monitoring started 13 mo after the valley had been planted and the cutting of grasses and vines ceased. We sampled the herpetofauna in all

sites, except the old valley, between 26 February 2001 and 1 March 2002 ( $n = 12$  censuses). We included the old valley in this study a month later and we sampled the herpetofauna between 15 March 2001 and 1 March 2002 ( $n = 11$  censuses). Each census transect was located within one of the vegetation plots, except in the old valley, where the census transect was located between two vegetation plots that were separated by 5 m (Fig. 1, see *Environmental Characterization*). We conducted diurnal censuses between 0830 h and 1330 h, and nocturnal censuses between 1830 h and 0030 h along a  $3 \times 50$ -m transect in each site (Fig. 1). Each monthly census took two days, and the order of visits consisted of one day for the three valley sites and one day for the hilltop and hillside. To minimize any difference among habitats due to time of censuses, we alternated the order of visits to each habitat on a monthly basis.

### Environmental Characterization

We determined the density of woody vegetation (stems with diameter at breast height  $>1.0$  cm) in two  $10 \times 50$  m plots in the three reference sites, and in one  $10 \times 50$  m plot in the deforested and reforested valleys. We located each of the vegetation plots in the middle of each site to sample the woody vegetation most representative of each habitat. We established one vegetation plot in the middle of the deforested valley and the reforested valley because they were narrow (approximately 20 m in the widest side). We also estimated the percent ground cover (percentage cover of rocks, leaf litter, woody litter, herbs, shrubs, and bare soil) in 40 subplots ( $1 \times 1$  m) separated by 5 m at all sites. In the center of each subplot, we estimated canopy cover by eye as the percent cover of vegetation relative to sky background above the observer. In addition, canopy height in each subplot was measured with a clinometer, and we counted the number of sub-canopy and canopy layers. We determined the number of sub-canopy and canopy layers (range: 0–5) as the number of horizontal branches above the center point of each subplot. In addition, during each monthly herpetofaunal census, we measured air tem-

perature (C), relative humidity (%), and wind speed (km/hr) at 0.1 m and 2.0 m above ground in each site. We took the microclimate measurements diurnally and nocturnally at 10-m intervals along the 50-m census transects.

### *Data Analyses*

We used simple regression analyses to compare the coefficient of variation of temperature and relative humidity during the study period and to determine whether the variability in microclimate factors changed in the reforested valley compared with the other sites. Wind speed was excluded from regression analyses because three sites had many zeroes. The *T*<sup>+</sup> method with Gabriel's approximation, which computes lower and upper comparison limits for each sample mean, was used to perform unplanned comparisons among regression coefficients (Sokal and Rohlf, 1995). The *T*<sup>+</sup> method, a conservative method, is preferred when sample sizes are nearly equal. If the lower and upper limits among coefficients do not overlap, then the coefficients are significantly different (Sokal and Rohlf, 1995).

The relationship between microclimate variables and habitats was examined with Principal Components Analysis (PCA), and the changes of the composition of the herpetofaunal assemblage in the reforested valley were examined with Nonmetric Multidimensional Scaling (NMS) using PC-ORD, Version 4 (McCune and Mefford, 1999). Once the final ordination solutions were obtained from PCA and NMS, we combined results of PCA and NMS axes scores with partial correlation to assess the relationship between microclimate variables and the changes in the composition of the herpetofaunal assemblage in ordination space (we recommend McCune and Grace [2002] and references therein for further details on these techniques and relevant applications for similar ecological data sets). We used PCA because of the general linear relationships among microclimate variables. In addition, PCA can reduce a large set of correlated variables to a few variables, which simplifies the interpretation of environmental relationships with sites (McCune and Grace, 2002). Most ecological

data are multivariate in nature and the relationships between species and between species and environmental variables are frequently non-linear (McCune and Grace, 2002). For this reason, we used NMS because this method is based on ranked distances, which linearize relationships between species, and between species and habitat characteristics. Therefore, NMS may represent a more appropriate method for analyses of ecological data and should be used more frequently in ecological studies (Clarke, 1993; McCune and Grace, 2002).

The microclimate matrix for PCA consisted of columns representing the microclimate variables and rows representing the three reference sites, the deforested valley, and each census in the reforested valley. The microclimate variables included mean monthly values of diurnal and nocturnal temperature (C), relative humidity (%), and wind speed (km/hr) measured at 0.1 m and at 2.0 m height and the coefficient of variation of each variable. The cross-product matrix for PCA was determined by correlation coefficients. Appendix II includes PCA loadings of the significant principal components, which explained 92% of variance in ordination space, and the environmental variables that best explained the ordination solution.

The matrix for NMS analysis of species assemblages was constructed using species presence/absence data. Our interest was documenting the colonization of species in the reforested site, and comparing the species composition with the other sites. Therefore, the matrix consisted of columns representing species and rows representing the three reference sites, the deforested valley, and each of 12 censuses in the reforested valley. We used all species detected in the reference and the deforested sites because we assumed that all species were present at the beginning of the study, and the initial increase in species in these sites was a sampling effect and not faunal succession. In contrast, in the reforested valley, we assumed that all species could be detected because of the simpler vegetation structure, and thus the increase in species was attributed to faunal succession.

Nonmetric multidimensional scaling ordination was based on Sørensen (Bray-Curtis)



distance measure, which works well with presence/absence or abundance data (McCune and Grace, 2002). We used random starting configurations with a maximum of 6 axes, stability criterion = 0.00005, 50 permutations with real data, and Monte Carlo tests based on 50 permutations. The final ordination solution was determined after examining all possible solutions from Monte Carlo tests, which give the probability that the stress in a given solution was obtained by chance, and we chose the solution with the minimum number of dimensions (axes) that provided the lowest stress (i.e., an inverse measure of fit to the data) and lowest instability (i.e., the standard deviation of stress) over 500 iterations. Once the final NMS ordination solution was obtained, we showed the two axes that explained most of the variation in ordination space and performed a cluster analysis to define groups of members (e.g., censuses/site or sites) based on their similarities in this solution. We used the Sørensen (Bray-Curtis) distance and the group average as the linkage methods and Multi-response Permutation Procedures (MRPP) to test for the grouping solution that represents the best structure of groups in ordination space. We applied MRPP for each grouping solution in ascending order, and we selected the grouping solution with the largest *A* statistic. The *A* statistic is a measure of observed-group homogeneity compared to random homogeneity (McCune and Grace, 2002), which allows for hypothesis testing in clustering analysis. This statistic assumes values from  $-1$  to  $1$ . In ecological data, values of  $A > 0.3$  are high and can be interpreted as groups whose members are more similar within than among groups.

We studied the development of the structure of the species assemblage in the reforested valley and compared it with the structure of the three reference sites and the deforested valley. We characterized the structure using the density of individuals of species within five trophic/habitat guilds. Root (1967) defined guilds as groups of species that are likely to compete for similar ecological resources in similar ways. Following Root's definition, we defined five trophic/habitat guilds based on our observations and other studies (e.g., Reagan, 1996; Rivero, 1998;

Roughgarden, 1995; Stewart and Woolbright, 1996; Thomas and Kessler, 1996). The five guilds are (1) reptiles that are insectivorous and occur in herbaceous habitats, (2) amphibians that are insectivorous and occur in herbaceous habitats, (3) reptiles that are insectivorous and occur in arboreal habitats, (4) amphibians that are insectivorous and occur in arboreal habitats, and (5) carnivores and one noncarnivorous species that occur in forests (= interior species). In guild 5, carnivores also are interior species, while the noncarnivorous species is found mainly in closed-canopy forests. We justify the combination of carnivores and the noncarnivorous species in guild 5 because the noncarnivorous species occur in very low abundance and its inclusion in a different guild would not clarify the general structure of species assemblages.

To determine whether the structure of the species assemblage in the reforested valley changed through time in comparison with the reference sites and deforested valley we used the  $G_{adj}$ -test of independence with William's correction for small sample sizes (Sokal and Rohlf, 1995). For this test, we used the percent mean density of individuals within each guild during March–June 2001, July–October 2001, November 2001–February 2002, and June 2003–September 2003.

## RESULTS

### *Species Sampling*

We recorded 16 species of amphibians and reptiles in the five habitats (Table 1). Specifically, we observed two species in the deforested valley, 11 species in the reforested valley, old valley, and karst hilltop, and 12 species in the karst hillside. Five species were shared among four habitats, and three species were unique to one habitat (Table 1). Of the shared species, the crested anole, *Anolis cristatellus* and the common coqui, *Eleutherodactylus coqui* were the most abundant species. Of the unique species, *Anolis pulchellus* was the most abundant species, and it occurred only in the reforested valley.

The combined mean density of amphibians and reptiles in a single site was highest in the karst hillside (1811.2 individuals  $ha^{-1}$ ) (Ta-

TABLE 1.—Distribution and mean monthly density (individuals ha<sup>-1</sup>) of amphibians (A) and reptiles (R) between February 2001 and February 2002 in the five habitats and the guild of each species. The niche guild includes the trophic level, habitat use, and diel activity of each species. Numbers in parenthesis after the trophic category represent the throphic/habitat guild used in analyses of assemblage structure. All species reproduce by terrestrial eggs except the Puerto Rican boa, *Epicrates inornatus*, which is viviparous. The reproductive mode of amphibians includes direct development (*Eleutherodactylus* sp.), eggs in a terrestrial foam nest and tadpoles develop either in the nest or in ponds that form after rain (*Leptodactylus albilabris*), and eggs deposited in water where tadpoles finish their development (*B. marinus*). \* We observed *Ameiva exsul* in the old valley but outside of the census transect. \*\* These species were detected between June and September 2003

Species	Habitat					Niche guild		
	Deforested valley	Reforested valley	Old valley	Karst hilltop	Karst hillside	Trophic	Habitat use	Diel activity
<i>Leptodactylus albilabris</i> (A)	11.1	22.2	6.1	0	0	Insect. (2)	ground	nocturnal
<i>Bufo marinus</i> (A)	5.6	0	0	0	0	Insect. (2)	ground	nocturnal
<i>Anolis pulchellus</i> (R)	**	739.0	0	0	0	Insect. (1)	herbs/grasses	diurnal
<i>Eleutherodactylus antillensis</i> (A)	**	177.8	0	144.4	33.3	Insect. (2)	herbs/grasses	nocturnal
<i>A. krugi</i> (R)	**	177.8	36.4	5.6	77.8	Insect. (1)	herbs/shrubs	diurnal
<i>A. cristatellus</i> (R)	**	88.9	357.6	894.4	1255.6	Insect. (3)	arboreal	diurnal
<i>E. cochranae</i> (A)	0	55.6	127.3	111.1	11.1	Insect. (4)	arboreal	nocturnal
<i>E. coqui</i> (A)	**	72.2	909.1	16.7	77.8	Insect. (4)	arboreal	nocturnal
<i>A. cuvieri</i> (R)	0	5.6	16.7	44.4	33.3	Carniv. (5)	arboreal <sup>1</sup>	diurnal
<i>A. evermanni</i> (R)	0	5.6	5.6	0	94.4	Insect. (3)	arboreal <sup>1</sup>	diurnal
<i>Epicrates inornatus</i> (R)	0	5.6	5.6	5.6	0	Carniv. (5)	ground/ arboreal <sup>1</sup>	nocturnal
<i>Alsophis portoricensis</i> (R)	0	5.6	0	5.6	11.1	Carniv. (5)	ground <sup>1</sup>	diurnal
<i>Ameiva exsul</i> (R)	0	0	*	5.6	5.6	Omniv. (1)	ground	diurnal
<i>A. stratulus</i> (R)	0	0	72.7	338.9	188.9	Insect. (3)	arboreal	diurnal
<i>Arrhyton exiguum</i> (R)	0	0	5.6	11.1	16.7	Carniv. (5)	ground <sup>1</sup>	diurnal
<i>Typhlops platycephalus</i> (R)	0	0	0	0	5.6	Insect. (5)	fossorial <sup>1</sup>	nocturnal?
Total	16.7	1355.9	1542.7	1583.4	1811.2			

<sup>1</sup> Forest-interior species.

ble 1). The combined mean density of amphibians and reptiles was similar between the karst hilltop and the old valley (1583.4 and 1542.7 individuals ha<sup>-1</sup>, respectively). The mean density of amphibians and reptiles was lower in the reforested valley (1355.9 individuals ha<sup>-1</sup>) than it was in the reference sites. The group of species that dominates the herpetofauna varied among sites. For example, arboreal reptiles were more abundant in the karst hillside, and represented 86.8% of the individuals in the local herpetofauna. Similarly, arboreal reptiles were more abundant in the karst hilltop, and represented 81.0% of the individuals. In contrast, arboreal amphibians were more abundant in the old valley, and represented 67.2% of the individuals. In the reforested valley, herbaceous reptiles were more abundant, and represented 67.6% of the individuals in the local herpetofauna.

Environmental Characterization

In the reforested valley stem density increased from 1666 stems ha<sup>-1</sup> to 2220 stems ha<sup>-1</sup> in two years, but this was only 18.3% of the mean stem density in the reference sites (12,143 stems ha<sup>-1</sup>, Fig. 3A). Mean canopy height in the reforested valley was 2.5 m in comparison with 5.5 m in the reference sites (Fig. 3B). The mean number of canopy layers in the reforested valley was 0.5 layers compared with 2.3 layers in the reference sites. Although the reforestation increased woody vegetation cover in the reforested valley, herbaceous vines and grasses still dominated the ground cover (Fig. 3C). Specifically, grasses dominated the ground cover in the deforested valley, while epiphytes (bromeliads, orchids, and *Anthurium* sp.) dominated the ground cover in the reference sites. In contrast, rocks were more common in the karst hills than in the valleys (Fig. 3D).

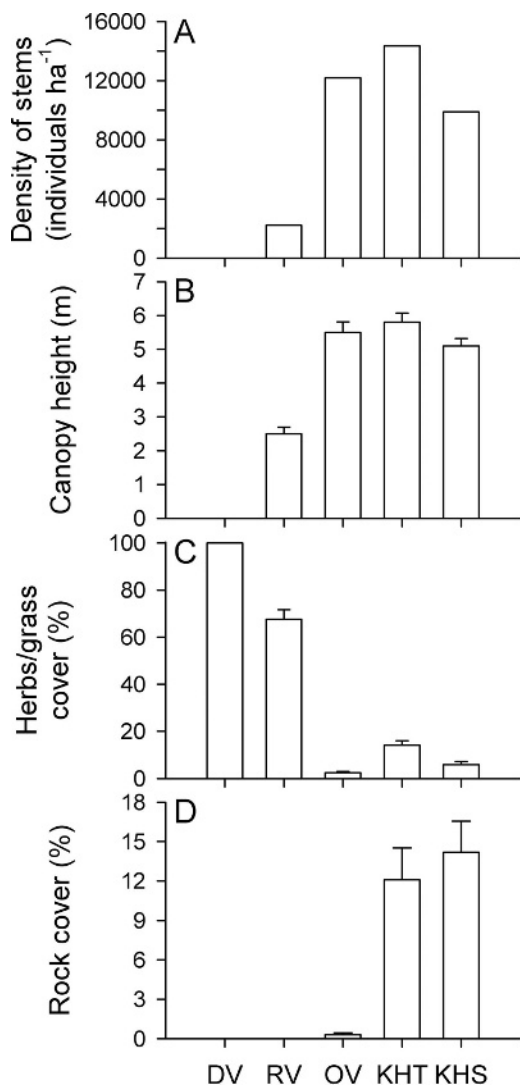


FIG. 3.—Vegetation characteristics: (A) Total density of stems >1 cm in diameter at breast height, (B) mean canopy height  $\pm$  SE, (C) mean percentage of herbs and grasses  $\pm$  SE, and (D) mean percentage of rocks  $\pm$  SE in the deforested valley (DV), the reforested valley (RV), and the reference sites (old valley = OV, karst hilltop = KHT, and karst hillside = KHS).

The cover of other substrates was correlated with woody vegetation. For example, leaf litter and woody litter were correlated positively with canopy height ( $n = 156$ :  $r = 0.5606$ ,  $P < 0.0001$ ;  $r = 0.1743$ ,  $P = 0.0296$ , respectively) and showed a pattern similar to the density of stems and canopy height among sites. Shrub cover was negatively correlated with canopy

height ( $r = -0.2009$ ,  $P = 0.0119$ ,  $n = 156$ ) and showed a pattern similar to the herbs/grass cover among sites.

Microclimate conditions varied among sites (Table 2). Mean temperature was highest in the reforested valley (27.6 C) and lowest in the old valley (26.6 C). In contrast, the old valley had the highest mean relative humidity (87.7%) while the karst hilltop had the lowest mean relative humidity (78.6%). The deforested valley had the highest mean wind speed (4.30 km/hr) followed by the reforested valley (1.11 km/hr).

Although the microclimate values in the reforested valley were within the range of the other sites (Table 2), the relationship between the monthly coefficient of variation of temperature and time varied among sites ( $F_{4,49} = 3.52$ ,  $P = 0.0134$ ) (Fig. 4A). Multiple comparisons among pairs of means ( $T'$  method) of the coefficient of variation in temperature differentiated the reforested valley from the deforested valley and the three reference sites. Specifically, the mean of the variation in temperature did not change in the deforested valley or in the reference sites through time. In contrast, the mean variation in temperature was significantly different in the reforested valley: at the beginning of the study, the variation of temperature in this valley was approximately two times greater than the reference sites, but by the end of the study, the variability declined to levels similar to the reference sites (Fig. 4A). A different relationship resulted in the variability of relative humidity among all sites (Fig. 4B). Although the variability of relative humidity decreased also in the reforested valley, the regression slope was not significantly different in comparison with the reference sites ( $F_{4,49} = 1.41$ ,  $P = 0.2453$ ) (Fig. 4B).

Principal Components Analysis (PCA) extracted five components with eigenvalues greater than 8% of the variance from the microclimate matrix, and the first two components explained 46.9% of the variation (Fig. 5A, Appendix II). The mean diurnal relative humidity at 10 cm, its coefficient of variation, and the nocturnal temperature at 10 cm had the highest loadings on component 1 (Appendix II). The old valley, karst hillside, and several late censuses in the reforested

TABLE 2.—Mean values  $\pm$  SE of microclimate variables in the reforested valley, deforested valley, and the reference sites between February 2001 and March 2002.

Habitat	Microclimate variable		
	Temperature (C)	Relative humidity (%)	Wind speed (km/hr)
Reforested Valley	27.6 $\pm$ 0.23	82.7 $\pm$ 0.77	1.11 $\pm$ 0.14
Deforested Valley	26.7 $\pm$ 0.18	84.6 $\pm$ 0.71	4.30 $\pm$ 0.27
Old Valley	26.6 $\pm$ 0.13	87.7 $\pm$ 0.48	0.24 $\pm$ 0.05
Karst Hilltop	27.4 $\pm$ 0.16	78.6 $\pm$ 0.58	1.52 $\pm$ 0.11
Karst Hillside	27.0 $\pm$ 0.14	83.8 $\pm$ 0.54	0.32 $\pm$ 0.05

valley were characterized by high diurnal relative humidity at 10 cm and high nocturnal temperature at 10 cm (i.e., negative scores of PC 1) (Fig. 5A). In contrast, early censuses in the reforested valley were characterized by high variability of relative humidity at 10 cm (i.e., positive scores of PC 1). Diurnal and nocturnal wind speed at 10 cm, and nocturnal wind speed at 2 m had the highest loadings on component 2 (Appendix II). The deforested valley, karst hilltop, and few early censuses in the reforested valley were characterized by high diurnal and nocturnal wind speed at 10 cm, and high nocturnal wind speed at 2 m (i.e., positive scores of PC 2) (Fig. 5A).

Composition and Structure of  
Herpetofaunal Assemblages

Nonmetric Multidimensional Scaling (NMS) analysis extracted two axes that explained 93.5% of the variance in ordination space (Fig. 5B). NMS axis 1 and 2 explained 26.7% and 66.8% of the variance, respectively. The presence of only two species in the deforested valley (see Table 1) resulted in a high dissimilarity in the ordination solution (Fig. 5B insert). Wind speed had the highest loadings in PC 2 (diurnal wind at 10 cm, and nocturnal wind at 10 cm and 2 m, Appendix II) and partial correlation revealed that wind speed separated the deforested valley from the rest of the sites along NMS axis 2 (Fig. 5B, insert). Excluding the deforested valley for visual clarity in NMS revealed that three groups had similar within-group homogeneity ( $A = 0.62, P < 0.0001$ ). Group 1 included censuses 1 to 7 in the reforested valley and group 2 included censuses 8 to 12 also in the reforested valley (Fig. 5B). Group 3 consisted of the three reference sites (forests >30 yr) which had a similar species composition. Partial correlation revealed that principal component of only PCA axis 1 correlated with scores of NMS axis 1 (deforested valley excluded;  $r = 0.7897, P < 0.0005, n = 15$ ), and three microclimate factors characterized the grouping of sites and census/site. High variation in diurnal relative humidity at 10 cm characterized group 1 along the right portion of the horizontal NMS axis 1. Higher diurnal relative humidity and nocturnal temperature at 10 cm characterized groups 2 and 3, respectively, along the left portion of the horizontal NMS axis 1 (Fig. 5B).

The community structure in the reforested valley included five trophic/habitat guilds that were represented by *Anolis krugi* and *A.*

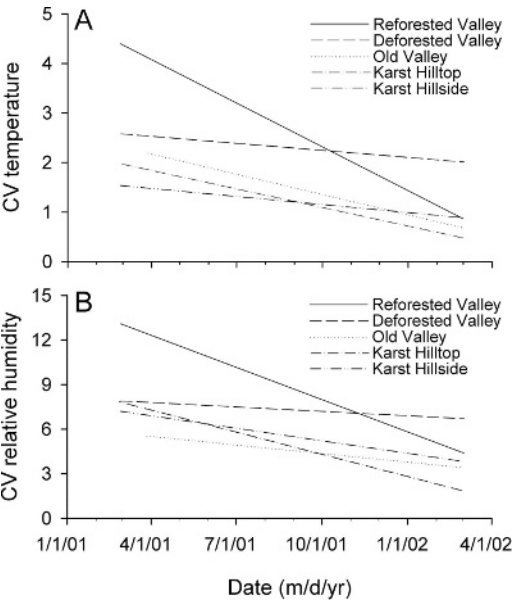


FIG. 4.—Regression of the coefficient of variation of (A) temperature and (B) relative humidity from February 2001 to March 2002 in all sites. We have shown only the regression lines to highlight trends.



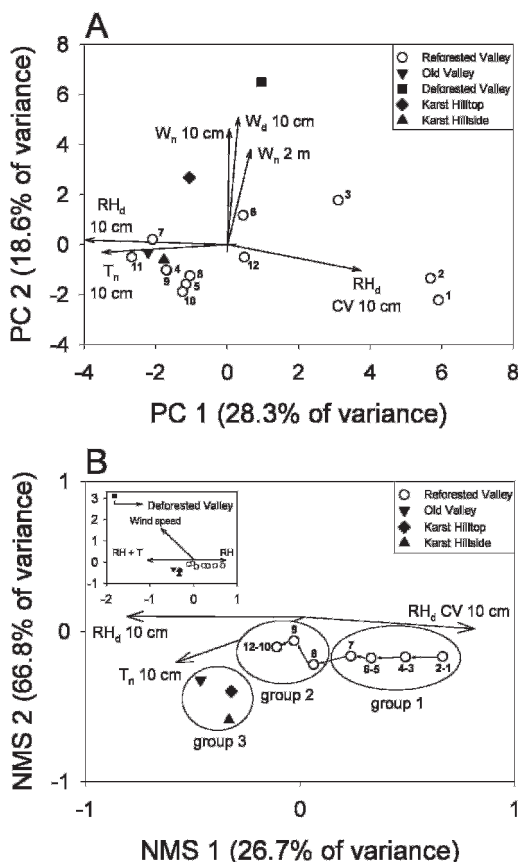


FIG. 5.—Ordination solutions: (A) Principal Component Analysis (PCA) and (B) Nonmetric Multidimensional Scaling (NMS). PCA ordination solution is shown only with the first two components and represents habitat/census in the reforested valley and habitat scores of the reference sites based on microclimate factors. Numbers at the right side of open circles represent the censuses in chronological order in the reforested valley. Vectors represent the direction and strength of microclimate factors that correlated significantly with the first two components. There were only two species in the deforested valley, which resulted in a high dissimilarity in the NMS ordination solution (insert), and the cumulative changes in species richness in the reforested valley and the total number of species in the three reference sites are shown without the deforested valley for visual clarity. In the reforested valley, open circles are connected with arrow lines to show the direction of the chronological changes in the composition of species assemblages. Ellipses group statistically significant censuses with similar within-variation in ordination space. Vectors represent the direction and strength of microclimate factors from PCA that correlated significantly with NMS axes scores of sites and site/censuses.

*pulchellus* (guild 1, insectivorous reptiles in herbaceous habitats), *Eleutherodactylus antillensis* and *Leptodactylus albilabris* (guild 2, insectivorous amphibians in herbaceous habitats), *A. cristatellus*, *A. evermanni*, and *A. stratulus* (guild 3, insectivorous reptiles in arboreal habitats), *Eleutherodactylus cochraniae* and *E. coqui* (guild 4, insectivorous amphibians in arboreal habitats), and the carnivorous and interior species *A. cuvieri*, *Epicrates inornatus*, *Alsophis portoricensis*, and *Arrhyton exiguum*, and the noncarnivorous interior species *Typhlops platycephalus* (guild 5, carnivores and/or interior species in forests). The assemblage structure in the reforested valley changed significantly during the study ( $G_{adj} = 118.41$ ,  $df = 12$ ,  $P < 0.0001$ ) (Fig. 6). From March to June 2001, insectivore reptiles in guild 1 characterized the reforested valley, and there was a lower density of insectivore reptiles in guild 3. Amphibians in guild 2 and guild 4 colonized between July and October 2001 (Fig. 6). Between November 2001 and February 2002 species of guild 5 colonized the reforested valley (i.e., the carnivorous giant anole, *Anolis cuvieri*, the Puerto Rican boa, *Epicrates inornatus*, and the racer, *Alsophis portoricensis*) (Fig. 6). Between June and September 2003, all guilds were still present in the reforested valley, but the density of individuals in each guild changed significantly from 2002 and 2003 ( $G_{adj} = 49.16$ ,  $df = 4$ ,  $P < 0.0001$ ). Specifically, the density of insectivore reptiles in arboreal habitats (i.e., guild 3) was greater than the density of insectivore reptiles in herbaceous habitats (i.e., guild 1) in the reforested valley (Fig. 6). In contrast, the assemblage structure in the deforested valley did not change between 2001 and 2002 (Fig. 6, Table 2). Between June and September 2003 two species in guild 1 colonized the deforested valley (i.e., *A. pulchellus* and *A. krugi*).

There was little change in the structure of the species assemblage in the reference sites (Fig. 6). The structure of the species assemblage in the karst hilltop did not change significantly from March 2001 to September 2003 ( $G_{adj} = 12.70$ ,  $df = 12$ ,  $P = 0.3914$ ) (Fig. 6). Similarly, the structure of the species assemblage in the karst hillside did not change

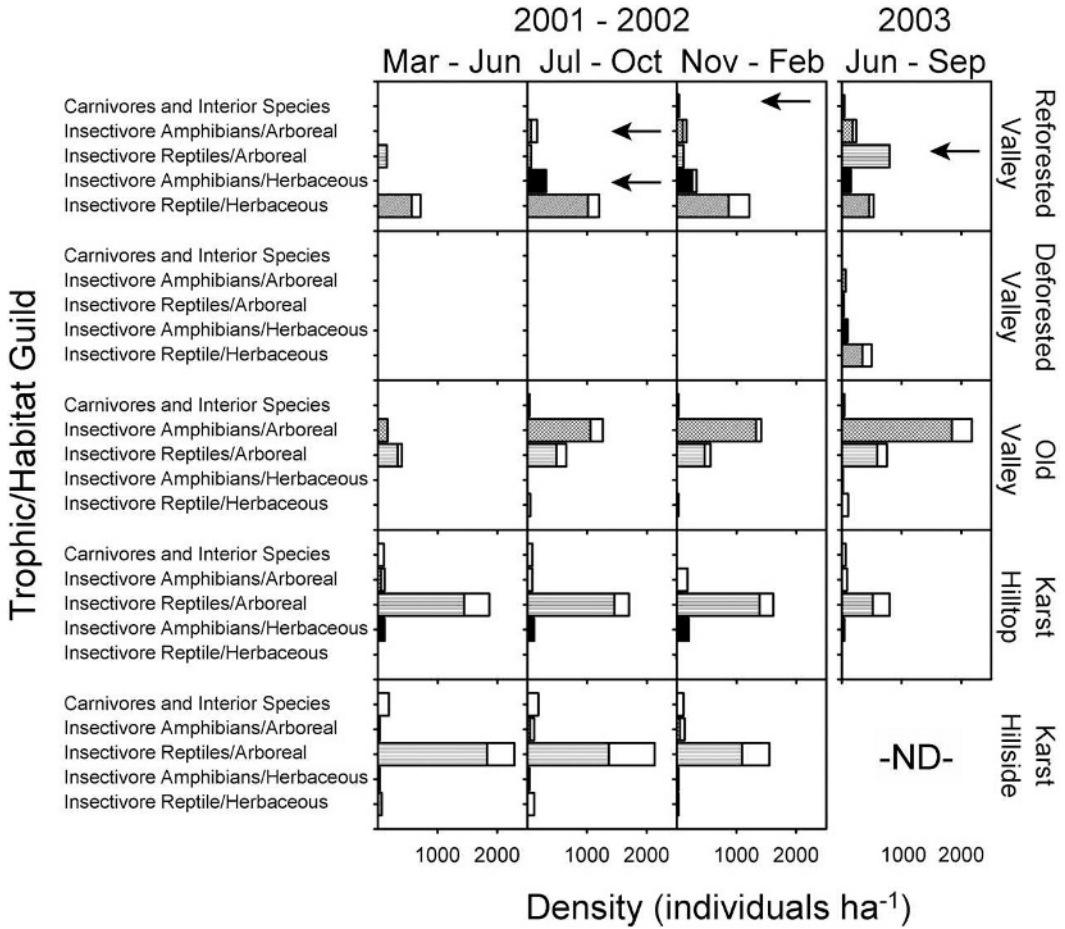


FIG. 6.—A comparison of changes in the structure of species assemblage during herpetofaunal succession in the reforested valley, the deforested valley, and the three reference sites. Horizontal bars represent the mean density of individuals in each of five trophic/habitat niche guilds, at three periods from March 2001 to February 2002 in each site, and during June and September 2003 except the hillside. Fill patterns in bars represent the most abundant species in each guild: backslash in guild 1 (insectivore reptiles in herbaceous habitat) = *Anolis pulchellus*, solid black in guild 2 (insectivore amphibians in herbaceous habitat) = *Eleutherodactylus antillensis*, horizontal lines in guild 3 (insectivore reptiles in arboreal habitats) = *A. cristatellus*, reticulate in guild 4 (insectivore amphibians in arboreal habitats) = *E. coqui*. Arrows highlights guilds that appeared and persisted in the reforested valley, and species replacement between guilds of reptiles in this valley: the insectivore/arboreal reptile guild has replaced the herbaceous/insectivore reptile guild as the most abundant guild by 2003.

from March 2001 to February 2002 ( $G_{adj} = 5.74$ ,  $df = 8$ ,  $P = 0.6763$ ) (Fig. 6). In these hills, insectivore reptiles in guild 3 characterized the local herpetofauna. The species assemblage of the old valley changed between the first two periods ( $G_{adj} = 40.98$ ,  $df = 12$ ,  $P < 0.0001$ ). During the first period (March to June 2001) insectivorous reptiles in guild 3 (arboreal habitats) characterized the old valley, and amphibians in guild 4 represented a smaller proportion of the structure (Fig. 6).

By the next period, the density of amphibians in guild 4 increased and became the most abundant guild; the structure did not change in any of the subsequent censuses (Fig. 6).

#### DISCUSSION

##### *Observed Pattern of Herpetofaunal Succession: Early Stages of Faunal Succession*

Herpetofaunal succession was greatly accelerated by planting woody seedlings. In only

13 mo, herpetofaunal richness increased from three to eleven species in the reforested valley. In contrast, in the deforested valley, which is under natural secondary succession, herpetofaunal richness did not increase during the same period and included only two species (*Leptodactylus albilabris*, *Bufo marinus*). The increase in herpetofauna in the reforested valley was related to the increase in vegetation heterogeneity, similar to the relationship between vertebrate succession and vegetation in chronosequences (e.g., birds, Bersier and Meyer, 1995; Johnston and Odum, 1956; mammals, August, 1983; Bustos, 1995; Schweiger et al., 2000; Williams et al., 2002; litter-dwelling tropical herpetofauna, Heinen, 1992).

Along with an increase in the richness of herpetofauna, the increase in vegetation heterogeneity in the reforested valley resulted in a change in the most abundant reptile, but not in amphibians. Initially, *Anolis pulchellus* was the most abundant reptile when the site was still dominated by herbaceous vegetation. As the woody vegetation cover increased, the arboreal species *A. cristatellus* replaced *A. pulchellus* as the most abundant reptile, approximately two years after the woody vegetation was planted (Fig. 6). In contrast, *Eleutherodactylus antillensis*, another grassland species, was the most abundant amphibian in the reforested valley early in the study period, and as woody vegetation cover increased, the arboreal *E. coqui* also colonized the valley, but it did not replace *E. antillensis* as the most abundant amphibian. The difference in species replacement between reptiles and amphibians is possibly due to differences in their microclimate requirements, which could lead to different patterns of herpetofaunal composition during early stages of succession.

The effect of temperature on physiology influences habitat use in reptiles (Miles, 1994). For example, *Anolis* spp. that occupy the warmest thermal niches have a high standard metabolic rate (i.e., an estimate of energy expenditure for maintenance), and in Puerto Rico, *Anolis pulchellus* has the highest standard metabolic rate and is the most abundant reptile in herbaceous and open habitats (Rand, 1964; Rogowitz, 2003). In

contrast, *A. cristatellus* is the most abundant reptile in closed-canopy forests, and has a lower standard metabolic rate (Rogowitz, 2003). The difference in the thermal physiology between these species explains why *A. pulchellus* was the most abundant reptile in the reforested valley at the beginning of the study when temperature was high and variable (Fig. 4A). Once the thermal conditions in the reforested valley became less variable and similar to the closed-canopy forest, *A. cristatellus* replaced *A. pulchellus* suggesting that changes in microclimate are important drivers of species replacement.

Conditions of high humidity facilitate rehydration, decrease the probability of egg desiccation, and facilitate the normal development of eggs in amphibians, particularly for species that produce terrestrial eggs, such as *Eleutherodactylus* spp. (Beuchat et al., 1984; Duellman and Trueb, 1994; Taigen et al., 1984). In Puerto Rico, *Eleutherodactylus* species that occur in open and disturbed habitats are species that can rehydrate faster at higher temperatures than species in closed canopy forests (van Berkum et al., 1982). *Eleutherodactylus antillensis* rehydrates faster at high temperatures than other Puerto Rican *Eleutherodactylus* (van Berkum et al., 1982), and this species was the most abundant amphibian in the reforested valley after the initial planting. In contrast, *E. coqui* rehydrates slower and is more susceptible to low humidity and high temperatures than *E. antillensis* (van Berkum et al., 1982). Although humidity has increased in the reforested valley, it is still highly variable (Fig. 4B), and *E. coqui* has not replaced *E. antillensis* as the most abundant amphibian. As the vegetation cover in the reforested valley increases, humidity will increase and become less variable (e.g., old valley), which should result in *E. coqui* replacing *E. antillensis*.

#### *Observed Pattern of Herpetofaunal Succession: Late Succession Species*

We have emphasized the influence of microclimate conditions on the pattern of species replacement in the reforested valley during early stages of succession, but other factors will also influence the development of species assemblage during succession. For

example, the herpetofaunal structure changed slowly, probably because of the lag time between initial colonization, the establishment of viable populations, and the availability of prey. Although the planted vegetation and the related changes in microclimate conditions provided a suitable environment for early colonizing species (e.g., *Anolis pulchellus* and *Eleutherodactylus antillensis*) (Table 1), the abundance and persistence of these species provided colonization opportunities for late succession species which prey upon them. Late succession herpetofaunal species included carnivores mainly found in closed-canopy forests like the diurnal giant anole, *Anolis cuvieri*, the common racer, *Alsophis portoricensis*, and the nocturnal boa, *Epicrates inornatus* (Table 1), and the diet of these carnivores frequently includes reptiles and amphibians in both arboreal and herbaceous habitats (Reagan, 1996; Thomas and Kessler, 1996). Given that we observed adults and juveniles of *A. cuvieri* and adults of *A. portoricensis* repeatedly sleeping on branches of planted trees, while *E. inornatus* was found foraging in the planted trees, we suggest that these species may represent a late succession stage of the herpetofauna in the reforested valley. In only three years, the herpetofaunal trophic structure has become more complex with the increase in vegetation structure and the increase in prey availability (Fig. 6).

#### *Predicted Pattern of Herpetofaunal Succession and Assembly Rules*

The herpetofaunal composition in the three forested reference sites helps to illustrate how microclimate factors are associated with the organization of species assemblage in the reforested valley. The forested reference sites have similar vegetation characteristics (Fig. 3), but the proportion of reptiles and amphibians in each site differed due to differences in microclimate. Specifically, forested valleys are surrounded by hills that protect them from solar radiation and strong winds. Humid air sinks downhill and remains in the valleys for long periods and the old valley site is more humid and cooler than the hill sites (Table 2). These microclimate conditions are suitable for amphibians and explain why amphibians were more abundant in the

old valley (Table 1). In contrast, the steep topography of the hill sites increases water runoff and prevents the retention of humidity in the soil. Hillsides and hilltops are exposed to solar radiation and stronger winds, which prevent further retention of humidity. The hill sites are characterized by lower humidity, higher temperature, and higher wind speed (Table 2). These microclimate conditions are suitable for reptiles, and explain why reptiles characterize the local herpetofauna in the hills (Table 1). In the reforested valley, microclimate conditions are intermediate between the conditions found in the hills and in the old valley (Table 2). Similarly, the proportion in percent of reptiles and amphibians in the reforested valley is also intermediate between the proportions found in the hills and in the old valley. As vegetation succession continues in the reforested valley, microclimate conditions will change, and amphibians should eventually characterize the herpetofauna as humidity increases and temperature decreases.

This study suggests that the development of the herpetofaunal assemblage during succession can be partially described by two simple assembly rules similar to those found in other studies with land vertebrates (Brown and Southwood, 1987; Diamond, 1975; Lawton, 1987). First, herpetofaunal species richness increased during secondary succession as woody vegetation cover increased (e.g., vegetation stratification). This assembly rule illustrates the most general pattern described in studies of vertebrate succession with birds, mammals, and the litter-dwelling tropical herpetofauna. Second, the composition of the herpetofaunal assemblage changed rapidly during early stages of succession (Fig. 5B), while the trophic structure changed slowly during succession (Fig. 6). In this assembly rule, we suggest that the pattern of herpetofaunal organization in the reforested valley was determined by specific habitat requirements of different species during succession (e.g., arboreal species colonizing the valley after trees were planted; carnivores colonized the valley after preys were established). The differences in physiology between reptiles and amphibians, however, require us to expand this second assembly rule to describe patterns



of herpetofaunal succession due to microclimate. Specifically, we expect reptiles to dominate early stages of succession when conditions are drier and warmer, and amphibians should dominate later stages of succession when conditions become more humid and cooler.

Concepts of vertebrate succession are mainly based on studies of birds and mammals, and rarely include microclimate variables as important factors controlling the organization of faunal assemblages. Our study has shown that in addition to vegetation and food availability, microclimate variables explain patterns of herpetofaunal organization during early secondary succession. Given that amphibians and reptiles represent roughly 45% of land vertebrates (birds—38%, mammals—17%) (Pough et al., 2001), it is essential that we understand the factors influencing the development of herpetofaunal assemblages (Duellman, 1989). Global warming and changes in regional precipitation patterns are believed to be major factors associated with worldwide population decline and extinction of amphibians and reptiles (Donnelly and Crump, 1998; Pough et al., 2001; Pounds and Crump, 1994; Pounds et al., 1999;); therefore, the effectiveness of herpetofaunal conservation and restoration projects can be improved by taking into account the influence of microclimate variables on the recovery of amphibian and/or reptile assemblages, particularly in altered ecosystems (Blaustein et al., 2001; Carey et al., 2001; Lawton, 1991).

#### RESUMEN

Los conceptos de sucesión de comunidades de animales vertebrados están basados principalmente en estudios con pájaros y mamíferos. Para proveer un entendimiento más amplio sobre la organización y sucesión de ensamblajes de animales vertebrados estudiamos el desarrollo de un ensamblaje de herpetos en un proyecto de reforestación. Muestreamos mensualmente el ensamblaje de herpetos entre febrero de 2001 y marzo de 2002 y entre junio y septiembre de 2003 en un valle cárstico (calizo) reforestado y comparamos la composición y estructura de su ensamblaje de herpetos con la de tres hábitats de referencia y con la de un valle deforestado

en una región caliza de Puerto Rico. En el valle reforestado, la sucesión de herpetos es facilitada por el aumento en la heterogeneidad de la vegetación y por la disminución en la variabilidad del microclima. La riqueza de especies aumentó rápidamente de tres a once durante 13 meses, con las especies de depredadores colonizando el valle reforestado al final del estudio. La estructura trófica cambió más lento (1) con un aumento en la densidad de individuos de especies arbóreas con el aumento en la cubierta de la vegetación y (2) con el aumento de especies de depredadores con el aumento en la densidad de presas. El patrón de sucesión de herpetos puede ser descrito por una regla de ensamblaje que considere microclima como un controlador importante del desarrollo del ensamblaje de especies. Sugerimos que el incluir microclima en reglas de ensamblaje puede ayudarnos a ampliar nuestro entendimiento de los conceptos de sucesión de ensamblajes de vertebrados en hábitats terrestres.

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## APPENDIX I

Mean heights of native woody species planted in the reforested valley.

Species	Family	Number of plants	Mean height (cm) Jan 2000	Mean height (cm) Apr 2001	Mean height (cm) Apr 2002
<i>Andira inermis</i> (W. Wr.) DC.	Leguminosae	108	28	72	92
<i>Thespesia grandiflora</i> DC.	Malvaceae	107	34	107	202
<i>Manilkara bidentata</i> (A. DC.) A. Chev.	Sapotaceae	95	45	84	123
<i>Calophyllum calaba</i> L.	Guttiferae	60	32	101	159
<i>Tabebuia heterophylla</i> (DC.) Britt.	Bignoniaceae	51	58	123	153
<i>Guarea guidonia</i> (L.) Sleumer	Meliaceae	38	43	89	123
<i>Hymenaea courbaril</i> (L.)	Leguminosae	10	49	121	198
<i>Thouinia striata</i> Radlkofler	Sapindaceae	7	64	119	146
<i>Zanthoxylum martinicense</i> (Lam.) DC.	Rutaceae	6	33	103	144
<i>Cecropia schreberiana</i> Miq.	Moraceae	5	78	129	420
<i>Guapira fragans</i> (Dum.-Cours.) Little	Nyctaginaceae	4	68	108	150
<i>Hura crepitans</i> L.	Euphorbiaceae	4	110	198	343
<i>Roystonea borinquena</i> O. F. Cook	Araceae	4	81	168	257
<i>Casearia sylvestris</i> Swartz	Flacourtiaceae	3	124	215	242
<i>Citharexylum fruticosum</i> L.	Verbenaceae	3	73	180	135
<i>Bucida buceras</i> L.	Combretaceae	2	61	123	145
<i>Casearia guianensis</i> (Aublet) Urban	Flacourtiaceae	2	77	110	148
<i>Eugenia monticola</i> (Swartz) DC	Myrtaceae	2	68	105	143
<i>Ocotea</i> sp.	Lauraceae	2	22	60	85
<i>Cedrela odorata</i> L.	Meliaceae	1	60	90	110
<i>Faramea occidentales</i> (L.) A. Rich	Rubiaceae	1	166	200	240
<i>Pimenta racemosa</i> (Miller) J. W. Moore	Myrtaceae	1	85	180	160

APPENDIX II

Principal Component Analysis loadings of 15 microclimate variables for the first five components. These components explained 92% of the variance in ordination space. The three highest loadings in each component are shown in bold. CV stands for coefficient of variation.

Environmental measure	Eigenvectors				
	PC 1	PC 2	PC 3	PC 4	PC 5
Diurnal wind speed at 10 cm	0.05	<b>0.43</b>	−0.08	−0.06	0.14
Diurnal temperature at 10 cm	0.26	−0.16	0.01	− <b>0.38</b>	0.02
Diurnal temperature CV at 10 cm	0.19	−0.21	0.19	−0.10	<b>0.32</b>
Diurnal temperature at 2 m	0.18	−0.10	−0.11	− <b>0.46</b>	0.12
Diurnal relative humidity at 10 cm	− <b>0.34</b>	0.04	0.11	0.03	−0.04
Diurnal relative humidity CV at 10 cm	<b>0.30</b>	−0.18	−0.01	−0.19	0.17
Diurnal relative humidity CV at 2 m	0.11	−0.11	0.13	0.26	<b>0.41</b>
Nocturnal wind speed at 10 cm	0.02	<b>0.41</b>	−0.11	−0.09	0.15
Nocturnal wind speed at 2 m	0.10	<b>0.38</b>	−0.10	−0.02	0.04
Nocturnal temperature at 10 cm	− <b>0.31</b>	−0.09	−0.05	−0.13	0.31
Nocturnal temperature CV at 10 cm	0.28	−0.09	0.00	<b>0.31</b>	−0.04
Nocturnal temperature CV at 2 m	−0.09	−0.23	− <b>0.32</b>	−0.17	−0.26
Nocturnal relative humidity at 10 cm	0.04	0.08	0.29	−0.31	− <b>0.33</b>
Nocturnal relative humidity at 2 m	0.00	0.04	<b>0.53</b>	−0.14	−0.18
Nocturnal relative humidity CV at 2 m	0.00	−0.20	− <b>0.44</b>	0.01	−0.16