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THE ROLE OF DISTURBED CARIBBEAN DRY FOREST FRAGMENTS IN THE SURVIVAL OF NATIVE PLANT DIVERSITY

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IAN ALFRED RAMJOHN

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Major Professor's Signature

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THE ROLE OF DISTURBED CARIBBEAN DRY FOREST FRAGMENTS IN THE SURVIVIAL OF NATIVE PLANT DIVERSITY

By

Ian Alfred Ramjohn

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ABSTRACT

THE ROLE OF TROPICAL DRY FOREST FRAGMENTS IN THE SURVIVAL OF NATIVE PLANT DIVERSITY

By

Ian Alfred Ramjohn

Tropical dry forests are a globally endangered ecosystem. Like most dry forests, those along the south coast of Puerto Rico have experienced a long history of disturbance and are restricted to a single large (4000-ha) protected area and an array of smaller fragments. Evidence suggests that small fragments can play an important role in the survival of native plant diversity, especially in the absence of large protected areas. In 1993, forest cover stood at 16900 ha (23.2% of the overall dry forest life zone); 13100 ha (18.0%) was Closed Forest and 3800 ha (5.2%) was Open Forest. Nine distinct clusters of fragments were identified across the dry forest zone based on a separation distance of 500 m. Only one fragment was isolated by a distance of over 1 km.

In one of the few studies of its kind, an array of forty fragments (ranging in size from 6 x 10^{-3} ha to 1372 ha) formed the basis of a detailed study. Guánica Forest, the 4000-ha reserve, was selected as the reference community. Nineteen fragments were classified as Relict (>75% 'old growth'), three were classified as Mixed (25-75% 'old growth') and seventeen were classified as Regrowth (<25% 'old growth'). One fragment was unclassified. Even small Relict fragments were able to support species assemblages that were representative of those found in Guánica Forest. On average, more of the reference species (sampled from Guánica Forest) were present in Relict (54±3.6%; mean ± 1 standard error) than in Regrowth fragments (24±2.7%). Nineteen fragments

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supported >50% of the reference species and five fragments supported >75% of them. The smallest fragment which supported >50% of the reference species was 0.04 ha. The species that dominated the reference sites in Guánica Forest were present in most Relict fragments but were absent from most Regrowth fragments. Four of these species (*Gymnanthes lucida*, *Eugenia foetida*, *Croton humilis* and *C. discolor*) were present in 63-73% of Relict fragments but were only present in 6-13% of Regrowth fragments. Species richness was a function of fragment area and disturbance history. Clustering based on Jaccard similarity in species composition produced five distinct groups of fragments (and two unassigned sites). Three of these clusters consisted predominantly of Relict sites (including one group of coastal fragments) and two consisted predominantly of Regrowth sites (one dominated by *Leucaena leucocephala* and the other by *Pisonia albida*).

Like other dry forests, both the fragments and Guánica Forest consisted of high densities of small, multi-stemmed trees; between 0.2 and 5.2 $m^2 ha^{-1}$ (up to 55% of basal area) were accounted for by stems between 1 and 2.5 cm diameter at breast height (dbh). Forty-four percent of all trees were multi-stemmed. Trees averaged 2.43 stems per tree; multi-stemmed trees averaged 4.22 stems. Of the 53 rare or endangered species present in southwestern Puerto Rico, 12 turned up in at least one of the sampled fragments. Twenty-three fragments supported at least one rare or endangered species. Based on the presence or absence of plant species among fragments, six species were designated potential indicators of sites with high conservation value (*Antirhea acutata*, *Coccoloba diversifolia*, *Cordia rickseckeri*, *Guettarda krugii*, *Plumeria alba* and *Savia sessiliflora*).

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I would like to thank the property owners who allowed me to work on their land, especially Eddie Sepulveda, Miguel Canals, Roberto Carlo, Dr. Acosta and the Fas family.

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CHAPTER 1: INTRODUCTION

With a long history of human disturbance, the south coast of Puerto Rico is an excellent place to study the ecology of tropical dry forest fragments. Scattered across the landscape is an archipelago of fragments that vary in size, age and disturbance history. Like much of the world's tropical dry forest, only a small portion of the original ecosystem survives (Janzen 1988a, b, Allen 2000, Trejo and Dirzo 2000), and most of what survives is in small fragments. Unlike many other areas that have been studied to date, the fragmentation of this landscape is not a new phenomenon. While there is no way of knowing the extent to which the distribution of species among the fragments may be considered to represent a final "equilibrial" distribution, many of the early changes that have been documented elsewhere (*e.g.*, Laurance *et al.* 2002b) are likely to have already occurred in this system.

This array of fragments is complemented by Guánica Forest (Bosque Estatal de Guánica), a relatively large, well-studied protected area that forms the core of a UNESCO Man and the Biosphere Reserve. Although Guánica Forest is not a pristine dry forest, it forms the best reference against which to compare these fragments. During its history, Guánica Forest has experienced a wide range of disturbances including cutting for charcoal and fence-post production, plantation forestry based on exotic species (Lugo *et al.* 1978, Canals Mora 1990, Wadsworth 1990, Molina Colón 1998, Erickson *et al.* 2002) and agricultural crop production (based on corn, squash and peas; Erickson *et al.* 2002). The fact that Guánica Forest has experienced a range of impacts that are comparable to those experienced by the fragments makes it a better reference against which to c

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which to compare the effects of fragmentation. Had Guánica Forest been in a 'pristine' condition (if such a thing existed), it would be impossible to differentiate the effects of fragmentation from those of disturbance.

While the presence of dry forest fragments outside of Guánica Forest was known prior to the initiation of this project, little information was available about their species composition and habitat quality. This study addressed the question of what exists in these fragments – whether they supported forest cover that resembled that of 'intact' dry forest, or whether they supported species-poor communities dominated by exotic species – and tried to identify some of the factors that correlated with habitat quality.

Tropical deforestation constitutes a major threat to biodiversity (Wilson 1985, Whitmore and Sayer 1992). While some species are eliminated directly by the process of forest clearing, others survive in remnant patches. Among the species that were present initially, some will subsequently be lost as a consequence of post-isolation changes that occur in the fragments (Turner 1996, Laurance *et al.* 2002b). In addition to the direct effects of forest removal, deforestation also tends to result in the degradation of remnant habitat (Laurance *et al.* 2002b). Skole and Tucker (1994) estimated that while only 6% of the closed-cover Amazonian forests had been cleared by 1988, an additional 9% of the land area had been affected by fragmentation and edge-related phenomena. Between 1978 and 1988 twice as much land was subject to human-induced modification as was actually cleared (Skole and Tucker 1994).

It is likely that deforestation in Puerto Rico followed a similar pattern to what has been observed elsewhere in Latin America since the 1960s (Rudel *et al.* 2002). Deforestation along a forested frontier usually follows a pattern of selective logging

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('high grading') followed by the migration of settlers along the logging access roads (Bierregaard and Dale 1996, Turner *et al.* 2001, Laurance *et al.* 2002a). These settlers clear land for agriculture, usually a mixture of subsistence agriculture and cash crops (Boserup 1964, Browder 1996, Turner *et al.* 2001). Land is cultivated until its fertility declines sharply and then new land is cleared. Since secondary forest is usually easier to clear than primary forest (*e.g.*, Freeman, 1955 cited in Lawrence *et al.*, 1998), previously cleared land is frequently cultivated again once it has recovered to the stage where fertility has been restored (Kleinman *et al.* 1996, Turner *et al.* 2001). Repeated cultivation with too short a fallow can lead to permanent loss of fertility and subsequent invasion by fire prone grasses (*e.g.,* Albers and Goldbach 2000, Turner *et al.* 2001). Once this stage is reached, land is often turned over to large landowners who convert it to pasture (Rudel *et al.* 2002). In other areas, forest is directly converted, either to pasture or for the establishment of large-scale agricultural schemes often based on government subsidies (Geoghegan *et al.* 2001, Steininger *et al.* 2001a). Rudel *et al.* (2002) considered this "hollow frontier" model to reflect one of the major drivers of permanent deforestation since in these cases secondary forests are not allowed to reclaim the landscape once the agricultural frontier advances. On the other hand, Boserup (1964) considered agricultural intensification as a consequence of increasing population size to be the main driver of deforestation. Changes of both sorts have been documented in Amazonia (Browder 1988, Ozorio de Almeida 1992, Laurance 1999), but in the absence of a detailed historical study there is on way to determine whether either of these models describes the actual pattern of landscape transformation that occurred when Puerto Rico was initially deforested.

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Patterns of deforestation are similar in the wet and dry tropics, but deforestation usually begins sooner and is more complete in dry forest zones (Steininger *et al.* 2001b, Laurance *et al.* 2002b). Burn efficiencies are higher in tropical dry forests than in wetter forests; slash fires consume 60-90% of pre-burn biomass in dry forests in Mexico and Brazil, but only 40-60% of the biomass in wet forests (Kauffman *et al.* 2003). The higher fertility of dry forest soils and the fact that they are easily cleared makes them attractive for agriculture. An alternative pathway to deforestation observed in the seasonally dry tropics involves a process of gradual degradation through the combined action of grazing and fire (Uhl and Buschbacher 1985,Murphy and Lugo 1986a, Janzen 1988a, b, Nepstad *et al.* 1999, Blackmore and Vitousek 2000, Nepstad *et al.* 2001, Cochrane and Laurance 2002). Once grazing enters the equation the resulting forest is more fire-prone; removal of cattle also makes these forests even more fire-prone, since tall ungrazed grass is able to carry fire deeper into forest fragments (*e.g.*, Janzen 1988a, Johnson and Wedin 1997, Blackmore and Vitousek 2000).

As a group, dry forests are the most threatened biome in the Neotropics. Of the eleven major habitat types recognized by Dinerstein *et al.* (1995) in Latin America and the Caribbean, dry broadleaf forests were the most threatened with 28 of 31 ecoregions (90.3%) falling in the Critical or Endangered categories, with the other three (9.7%) falling in the Vulnerable or Relatively Stable categories (Dinerstein *et al.* 1995). In many cases, dry forest landscapes consist of little more than a scattering of disturbed fragments in a sea of deforestation (Janzen 1986, 1988b, Murphy and Lugo 1995, Murphy *et al.* 1995, Smith 1997, Allen 2000, Trejo and Dirzo 2000).

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Habitat Fragmentation and the Preservation of Biodiversity

Definition of Fragmentation

Some authors have used the term "fragmentation" synonymously with habitat destruction (*e.g.*, Andrén 1994) while others have used it to describe both habitat destruction and the processes by which the remnant habitat is broken into smaller pieces (*e.g.*, Diffendorfer *et al.* 1995, With and Crist 1995, With *et al.* 1997, Dooley and Bowers 1998). Others have used the term fragmentation in the narrow sense, clearly distinguishing between habitat destruction and fragmentation (*e.g.*, Bascompte and Solé 1995, McGarigal and McComb 1995, Lindenmayer and Possingham 1996, Nève *et al.* 1996). In this study the term "fragmentation" has been used in the second sense.

Bunnell (1999) considered the term 'habitat fragmentation' to include six discrete concepts. Modification of intact habitat may include (1) reduction of the total area; (2) increase in the amount of edge; (3) decrease in the amount of interior habitat; (4) isolation of a habitat fragment; (5) increase in the number of habitat fragments; and (6) decrease in the average size of a habitat fragment. Different taxa may respond in different, and even contradictory, ways to these processes, making "habitat fragmentation" a complex phenomenon (Haila 2002, Laurance *et al.* 2002b) . In addition, the term 'habitat fragment' is largely undefined in the literature. For the purpose of this dissertation, a habitat fragment is considered to be a unit of an ecosystem whose boundaries and associated conditions have been determined by human-influenced or other disturbances.

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Spatial Organization of Remnant Habitat

Habitat destruction tends to proceed in a non-uniform manner which leaves forest fragments concentrated in ravines, riparian strips, steep hillsides, fence lines and hedgerows (Forman 1995, Kahn and McDonald 1997, Lamb *et al.* 1997). One of the major debates in community ecology in the 1970s and 80s was the SLOSS debate – whether it is preferable to protect a Single Large or Several Small reserves (*e.g.*, Simberloff and Abele 1979, Wilcox and Murphy 1985). At the heart of the issue was the extent to which a certain amount of habitat distributed over several parcels was equivalent to the same area of habitat in a single parcel.

Over the last 22 years, the Biological Dynamics of Forest Fragments Project (BDFFP) near Manaus, Brazil, has convincingly demonstrated the value of large reserves in the humid tropics (Laurance *et al.* 2002b), although Thomas (2004) suggests that the BDFFP model represents an extreme case of sensitivity to fragmentation, and that forests in many other areas (such as Malaysia, where he worked) are much less sensitive to fragmentation. The fact that many species are rare and have patchy distributions (Hubbell 1979, Hubbell and Foster 1986, Pittman *et al.* 1999) makes the location of a fragment an important determinant of its ability to conserve biodiversity. The initial inclusion of a species in a fragment is essentially a sampling effect, although mobile species displaced by deforestation may move into remnant habitat (Bierregaard and Lovejoy 1989). Scattered fragments may also be able to sample more habitat types than can a large block of habitat, but they are not guaranteed to do so, since certain types of habitat are more prone to be cleared (Lamb *et al.* 1997). Kahn and McDonald (1997) suggested that three factors dictate where forest tends to persist – the physical nature of the terrain

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the terrain, the legal status of the land, and whether it is economically viable to convert it to non-forest uses. Deforestation is likely to concentrate on highly productive lowland areas which lack legal or cultural protection (Lebbie and Freudenberger 1996, Kahn and McDonald 1997, Lamb *et al.* 1997). Remnant fragments often occupy the least desirable land and may not provide suitable habitat for many species.

Fragment Area

Fragment area is a primary determinant of species richness (Arrhenius 1921, MacArthur and Wilson 1967, Rosenzweig 1995, Lomolino 2000, Whittaker *et al.* 2001). The size of a fragment will influence the number of species that are present when the fragment is created and the probability of species' persistence. Given the relatively short time frame of most fragmentation studies, area effects have mostly been demonstrated for animals, but some studies have also demonstrated this for plants (Leigh *et al.* 1993, Turner 1996). MacArthur and Wilson (1967) predicted that extinction rates should be negatively correlated with fragment area, a prediction that has been supported by the findings of the BDFFP study (Laurance *et al.* 2002b and references therein).

On the other hand, some studies have produced results that conflict with these predictions. As Thomas (2004) pointed out, patchily distributed species may be less sensitive to fragment area than are uniformly distributed species. Once a patchily distributed species is present in a fragment it is more likely to exist in a viable population than is an evenly dispersed species (which is likely to be uniformly rare throughout its range). Evenly dispersed species exist in populations that are a function of fragment area. In their review of fragmentation experiments, Debinski and Holt (2000) found many studies w

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studies which did not show an area effect, although they pointed out that many of them were carried out on a time-scale that may be too short to elicit area-driven changes in the community. In addition, Turner *et al.* (1996), Pither and Kellman (2002) and Thomas (2004) found that small tropical forest fragments were able to support a substantial proportion of the native community.

Edge Effects

Natural areas surrounded by human-altered landscapes are subject to "the eternal external threat" (Janzen 1986). The smaller the fragment, the more strongly it will be influenced by these external factors collectively termed "edge effects". One of the major consequences of habitat fragmentation is an increase in the proportion of edge in a landscape (Chen *et al.* 1992, Skole and Tucker 1994, Kapos *et al.* 1997). While larger sites are likely to consist of both "edge" and "interior" habitat, smaller sites may be entirely edge (Laurance 1991, Imre 2001).

Air temperature, air moisture, vapor pressure deficit (VPD), soil moisture, light intensity and levels of photosynthetically active radiation (PAR) change at edges. Kapos (1989) found differences in air temperature and VPD up to 60m into fragments at the BDFFP site in Amazonia but this distance decreased as the edge matured and became more closed (Williams-Linera 1990, MacDougall and Kellman 1992, Camargo and Kapos 1995, Kapos *et al.* 1997). Murcia (1995) considered orientation and physiognomy to be important in moderating the intensity of abiotic edge effects. While edge orientation is likely to be more significant at mid- to high latitude sites (*e.g.*, Palik and Murphy 1990, Matlack 1994), Turton and Freiburger (1997) found that abiotic factors

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were influenced more by edge aspect than by distance from the edge in a relatively low latitude (17° S) Australian forest fragment.

Wind is a major source of damage to trees along edges and unlike changes in microclimate, wind damage does not decline as edges age (Laurance *et al.* 2002b). When moving air encounters a forest edge, eddies are created upstream and turbulence downstream (Ghuman and Lal 1987) which can be powerful enough to break or uproot canopy trees (Williams-Linera 1990, Esseen 1994, Laurance 1997). As edges become older and less permeable, downwind turbulence increases (Savill 1983, Laurance 1997, Laurance *et al.* 2002b). Since fragments generally have a larger proportion of "edge" and a smaller proportion of "interior" than does continuous forest (Laurance 1991, Forman 1995, Imre 2001), one would expect to find more wind damage in fragments than in continuous forest. However, Van Bloem *et al.* (in press) found no significant difference in the amount of damage experienced by fragmented or continuous dry forest in Puerto Rico following Hurricane Georges in 1997.

High levels of tree mortality have been recorded near edges (Lovejoy *et al.* 1986, Laurance 1991, Leigh *et al.* 1993, Ferreira and Laurance 1997, Laurance *et al.* 1998, Mesquita *et al.* 1999, Laurance *et al.* 2002b). Higher levels of tree mortality and wind-throw result in an increase in disturbance-associated species (*e.g.*, the pioneer tree *Cecropia sciadophylla* increased 33-fold along the edges of the BDFFP fragments over a 20 year period; Laurance *et al.*, 2001). These changes, which have been termed hyperdynamism, result in an intrinsically less stable community in forest fragments (Laurance 2002, Laurance *et al.* 2002b).

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In contrast with the BDFFP model (which he calls the "things fall apart" model), Thomas (2004) pointed out that other studies (Kellman 1996, Kellman *et al.* 1996, Turner 1996, Turner and Corlett 1996, Corlett and Turner 1997, Harrington *et al.* 1997, Turner *et al.* 1997, Kellman *et al.* 1998, Pither and Kellman 2002) have found relatively slow rates of change in tropical forest fragments in some areas (what he calls the "more of the same" model) – in essence, that community change in forest fragments is driven by the same demographic processes that drive the dynamics of continuous blocks of forest. Thomas suggests that one of the important differences between the Amazonian fragments where Laurance formulated his theory and the Southeast Asian fragments where Thomas worked is one of wind velocity – Peninsular Malaysia experiences neither trade winds nor typhoons, while Central Amazonia experiences a continent interior "Amazon River Breeze" which commonly exceeds 15 km h^{-1}.

Edge effects may be experienced differently by dry forest fragments. Dry forests (especially in the insular Caribbean) have more open canopies than do wetter forests, allowing more light and wind penetration. These differences in canopy architecture are likely to affect interactions with air currents. The drier conditions may increase the effects of desiccation, but the fact that these trees are adapted to drier conditions may make the impact of this desiccation less severe. Research is needed to determine if the patterns of edge effects observed in wetter forests are the same for dry forests, or if there are qualitative differences between wet and dry forests. As Van Bloem and colleagues (Van Bloem *et al.* 2003, Van Bloem *et al.* in press) pointed out, Puerto Rican dry forest has a long history of wind disturbance via hurricanes and tropical storms, and is able to respond to wind disturbance through the production of sprouts even in undamaged trees

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(to which phenomenon they attribute the multi-stemmed nature of these forests). This history of wind disturbance in evolutionary time suggests that dry forests in the insular Caribbean are likely to be pre-adapted to the wind stresses that are likely to be associated with fragmentation. However, in the absence of any studies directly addressing edge-related phenomena in these forests this remains purely speculative. Despite the importance of edge-related phenomena in fragmentation studies, this study did not directly address edge-related questions.

Fragment Invasibility

Habitat fragments surrounded by a matrix of altered vegetation are susceptible to invasion by the species that dominate the matrix (Janzen 1983, 1986b, Hopkins *et al.* 1990, Laurance 1991, Fensham 1995). J. B. Kirkpatrick and L. Gilfedder (Kirkpatrick and Gilfedder 1995, Gilfedder and Kirkpatrick 1998) found that surrounding vegetation, together with grazing, were the major determinants of fragment integrity in subhumid Tasmanian habitat fragments. Willson and Crome (1989) found both animal-dispersed and wind-dispersed seeds were transported up to 80 m inward from the edge into Australian rainforest fragments.

The position of fragments on the landscape may also increase the probability of invasion by non-forest species. In open landscapes, forest fragments can be important roosting sites for birds and bats. The behavioral patterns of birds and bats concentrate seeds in roosting or feeding areas (Snow 1962, Livingston 1972, Howe and Primack 1975, Howe 1977, Fleming and Heithaus 1981, Glyphis *et al.* 1981, Uhl *et al.* 1981, Debussche *et al.* 1982, Uhl *et al.* 1982, McDonnell and Stiles 1983, Guevara *et al.* 1986, McClana

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McClanahan and Wolfe 1987, Janzen 1988a, Guevara *et al.* 1992, Guevara and Laborde 1993, McClanahan and Wolfe 1993, Guevara *et al.* 1998, Toh *et al.* 1999, Galindo-González *et al.* 2000). While much has been said about the ability of frugivorous birds to move seeds from forest fragments into abandoned pasture (da Silva *et al.* 1996, Martínez-Garza and González-Montagut 1999, Ortiz-Pulido *et al.* 2000) , little has been said about the ability of frugivores to move the seeds from the matrix into fragments (Aldrich and Hamrick 1998), despite the fact that this may be a significant factor in the degradation of isolated fragments.

Population Dynamics and Extinction

Rare species are usually assumed to have high extinction probabilities since small populations are at risk as a consequence of environmental or demographic stochasticity (Caughley 1994). The viability of small populations can also be affected by the loss of genetic diversity. Most tropical trees are outbreeders with complex incompatibility systems (Bawa 1974, Zapata and Arroyo 1978, Bawa *et al.* 1985, Bawa 1990). Since they are less prone to inbreeding in natural conditions, outbreeders are likely to carry a moderately high genetic load of slightly deleterious alleles (Lande 1995). Minimum viable population sizes for tropical forest trees needed to ensure long-term survival have been estimated at effective populations sizes (N_e)[1] of about 5000 (Alvarez-Buylla *et al.* 1996). However, the studies that led to these conclusions were not done on insular populations. Species native to the Greater and Lesser Antilles should be adapted to much

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[1] N_e is defined as the size of an idealised population that would have the same amount of inbreeding or random gene drift as a given real population (Kimura and Crow 1963, Alvarez-Buylla *et al.* 1996).

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smaller populations than are mainland populations; historically small populations are likely to be more inbred and, as a consequence of this, to carry lower genetic loads (Alvarez-Buylla *et al.* 1996). This makes them less susceptible to inbreeding depression (reduced viability, seed production and growth rates caused by the segregation of partially recessive lethal alleles). Species that are tightly tied to mutualists are at added risk because they are likely to go extinct if fragments do not support viable populations of the mutualist (Bond 1994, Nason *et al.* 1997). Species that are "seed limited" – those that depend on seed production to replace senescent stems – are likely to be at higher risk of extinction than are "resprouters", which depend primarily on sprouting to replace senescent stems (Kruger *et al.* 1997, Bond and Midgley 2001). These factors add levels of complexity beyond the simple assumptions relating rarity with extinction risk.

The spatial arrangement of fragments may also influence the ability of a fragmented system to maintain plant populations. The probability of extinction of an isolated population can be reduced as a consequence of immigration – the so-called 'rescue effect' (Brown and Kodric-Brown 1977). While the distance between fragments is likely to be a key factor in determining the amount of seed flow among fragments, there are few data as to the actual inter-fragment distances that birds and bats are likely to move seeds. Da Silva *et al.* (1996) found that most forest birds are unlikely to cross more than 100-200 m of open pasture. Graham's (2001) calculations suggest that toucans are unlikely to move more than 300 m across pasture. Lamb *et al.* (1997) stated that Australian birds are known to readily cross 500 m distances between fragments. While Ranta *et al.* (1998) used a distance of 350 m as a distance across which rainforest animals are unlikely to move, this value appears to be an assumption that was not tied to any

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specific data. The probability of a bird (or bat) actually transporting viable seed as it moves between fragments is also likely to decrease as the distance increases, since longer movements are likely to include stops at trees at various points between the fragments (Graham 2001), at which point seeds may be defecated or regurgitated, thus reducing the total volume of seed that the bird may be carrying.

Spatial and Temporal Scale

Most studies of habitat fragmentation have looked at systems that have a relatively short history of fragmentation (on a scale of a few years to a few decades; Turner *et al.* 1996, Debinski and Holt 2000) or very long time scales (a few thousand years; Morrison 2002, Pither and Kellman 2002). Few studies have looked at systems that have been fragmented on an intermediate time scale. In that regard, this study is unusual. In addition, few studies of forest fragments in the tropics have looked at small fragments; Pither and Kellman (2002) stated that only two published studies that they were aware of (theirs and Thomas, 2004) have looked at fragments 1 ha or smaller. In both of these regards then, this study is at a scale that is unlike that of other studies.

Puerto Rican Dry Forests

Tropical dry forests are one of the major tropical biomes. As defined by Holdridge (1967), dry forests may have once covered 42% of the land area in the tropics and subtropics (Brown and Lugo 1982). They are also among the most heavily impacted tropical forests (Lerdau *et al.* 1991). Dry forests have been settled longer than wetter forests, and deforestation has "preceded and exceeded that of evergreen forests"

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(Steininger *et a*l. 2001a). Human population densities are higher in drier regions than in the wetter parts of the tropics (Tosi and Voertman 1964). The dry forests of the wider Caribbean and Central America have been largely eliminated (*e.g.*, Janzen 1986b, Murphy and Lugo 1986a, Janzen 1988b, Kimber 1988, Dinerstein *et al.* 1995, Murphy and Lugo 1995, Gonzalez and Zak 1996, Gillespie 1999, Gillespie *et al.* 2000), as have those of the Caribbean coast of Venezuela and Colombia (Ceballos 1995, Dinerstein *et al.* 1995). Only 27% of the original dry forest remained in an intact state in Mexico in 1990 (Trejo and Dirzo 2000) and deforestation rates remained high. In South America, an arc of deciduous and semi-deciduous forests stretches from eastern Pará, Brazil to Santa Cruz, Bolivia (Steininger *et al.* 2001a). Most of this dry forest has been heavily affected by development, and the last remaining large block of dry forest, the Chiquitanía in Bolivia, is at present experiencing the highest rate of deforestation in the world (Steininger *et al.* 2001a, Steininger *et al.* 2001b).

Dry forests tend to be shorter in stature, have more open canopies and have greater stem densities (Murphy and Lugo 1986a) than do wetter forests. Canopy heights are, on average, 50% that of wet forests (10-40 m for dry forests vs. 20-84 m for wet forests; Murphy and Lugo 1986a) and basal areas are about 30-75% that of wet forests (17-40 m^2 ha^{-1} for dry forests *vs*. 20-75 m^2 ha^{-1} for wet forests; Murphy and Lugo 1986a). Productivity varies with soil moisture; net primary productivity is about 50-75% that of wet forests (Murphy and Lugo 1986a). Aboveground biomass is lower in dry forests (78000-32000 kg ha^{-1}) than in wetter forests (26900-118600 kg ha^{-1}), but dry forests have a greater proportion of their total biomass belowground (Murphy and Lugo 1986b). Dry forest soils tend to be richer in nutrients than wetter forest soils (Lugo and Mu

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and Murphy 1986a, Steininger *et al.* 2001a, Laurance *et al.* 2002a) and are thus preferred for agriculture.

These forests are often classified physiognomically on the basis of structure and degree of deciduousness (Schimper 1903, Beard 1944, 1955). Beard (1944, 1955) classified dry forests as semi-deciduous forest, deciduous forest, thorn forest and thorn scrub. Other definitions of dry forest have been made on climatic or bioclimatic bases. Bioclimatic definitions (*e.g.*, Holdridge 1967) include patches of more mesic forest within a more xeric overall community, such as gallery forests, within the overall definition of dry forests. Caribbean dry forests tend to be shorter in stature and have more open canopies than do Central American dry forest – a fact that has been attributed to the effects of hurricanes by some (*e.g.*, Van Bloem *et al.*, in press). Canyon and sinkhole forests in Guánica Forest, Puerto Rico are taller, less deciduous and have fewer stems per tree than do forests in more exposed areas (Lugo *et al.* 1978, Castilleja 1991, Farnsworth 1993). While the obvious explanation for this lies with the fact that canyon forests have more access to moisture, it is impossible to rule out a reduced hurricane impact in these more sheltered areas.

Sarmiento (1972) discussed the convergence between dry forests of northern and southern South America. Despite the fact that taxa are shared between the two regions (discussed by Pennington *et al.* 2000), dry forests of northern and southern South America are dominated by different genera. While Caribbean dry forests are characterized by genera typical of the northern Neotropics, Jamaica and Puerto Rican dry forests are unusual in that the dominant families (in terms of numbers of species) are the Myrtaceae and the Rubiaceae, while continental dry forests are dominated by the

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Leguminosae and the Bignoniaceae (Gentry 1995, Gillespie *et al.* 2000, Trejo and Dirzo 2002). While this in part reflects a radiation of the genus *Eugenia* in the Caribbean, the relative unimportance of legumes in intact Puerto Rican dry forest is striking.

Dry forests have been described as an "endangered ecosystem" (Janzen 1988b). Most dry forests have been highly impacted by agriculture and urbanization (Murphy *et al.* 1995). Caribbean dry forests remain under threat. Losses continue to be high in the Dominican Republic (Roth 1999, 2001). Deforestation in the Hellshire Hills, Jamaica's largest remaining tract of dry forest, was almost twice the national average between 1987 and 1992 (Tole 2002). Little intact dry forest remains in Puerto Rico or the Lesser Antilles (Kimber 1988, Ray 1993, Francis *et al.* 1994, Gonzalez 1994, Ray and Brown 1994, Murphy *et al.* 1995, Gonzalez and Zak 1996, Government of Grenada 2000). Dry forests in Grenada are threatened by housing development, fuel wood harvest, and tourism development (Government of Grenada 2000), in Tobago by tourism development (Boodram 2001) and in Trinidad by petroleum production, plantation forestry and agricultural encroachment (Ramjohn *et al.* 2002a, Ramjohn *et al.* 2002b, Ramjohn *et al.* 2003).

Puerto Rican dry forest remains among the best studied in the Caribbean. Guánica Forest, which was described as "an excellent example of subtropical dry forest" (Ewel and Whitmore 1973), is one of the major sites of dry forest research in the northern Neotropics. Five forest associations have been documented within Guánica Forest: mangrove forest, dwarf forest, dry scrub forest, deciduous forest and semi-evergreen forest (Lugo *et al.* 1978). The largest of these, the deciduous forest, is by far the best studied (Lugo *et al.* 1978, Dunevitz 1985, Murphy and Lugo 1986b, Castilleja 1991, Quigley

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Quigley 1994, Murphy and Lugo 1995, Dunphy 1997, Molina Colón 1998, Dunphy *et al.* 2000), but the community composition and metabolism have also been documented for the dry scrub forest and the semi-evergreen forest (Lugo *et al.* 1978, Castilleja 1991).

The deciduous forest association is dominated by *Gymnanthes lucida* Sw., *Exostema caribaeum* (Jacq.) R. & S., *Pisonia albida* (Heimerl) Britton ex Standl., *Coccoloba microstachya* Willd. and *Amyris elemifera* L. (Lugo *et al.* 1978, Murphy and Lugo 1986b, Castilleja 1991). The semi-evergreen forest association is dominated by *Gymnanthes lucida, Bucida buceras* L., *Bursera simaruba* (L.) Sarg. and *Pictetia aculeata* (Vahl) Urban (Lugo *et al.* 1978, Castilleja 1991). The scrub forest association is dominated by *Bucida buceras, Bursera simaruba, Pictetia aculeata, Thouinia striata* Radlk. in Engler & Prantl and *Pilosocereus royenii* (L.) Byles & Rowley (Lugo *et al.* 1978, Castilleja 1991).

Succession in Caribbean Dry Forest

Although the term succession is applied to the recovery process on both cut-over forests and those that have been converted to non-forest land uses and then abandoned, there are substantial differences in the pattern of succession between these two 'types' (Corlett 1994, Molina Colón 1998, Boucher *et al.* 2000, Mesquita *et al.* 2001 Burgos and Maass in review).

Corlett (1994) distinguished two groups of successional tropical forests – those that have regrown on land that was converted to a non-forest land-use prior to being abandoned, and those that have regrown on land that was disturbed but which was never fully converted to an alternative land-use. He suggests that the term 'secondary forest' should

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should only be applied to the former example since the latter type of forest usually still resembles primary forest in species composition, while the former type of forest tends to support a distinct community.

Forests that have simply been cut recover relatively quickly – on the order of 50-200 years – while intensively used agricultural land was estimated to require on the order of 500 years or more to recover (Guariguata and Ostertag 2001).

One of the major differences between cut and converted forests involves what Vandermeer *et al.* (1996) called the "direct regeneration pathway". In cut-over forest or lightly used agricultural land, rootstocks remain intact and are capable of sprouting. Dry forest trees are especially prone to be resprouters (Kruger *et al.* 1997, Bond and Midgley 2001), and are able to rapidly regenerate a discontinuous canopy dominated by the species that were present prior to being cut (Ewel 1971, Ewel 1980, Dunevitz 1985, Murphy and Lugo 1986b, Murphy *et al.* 1995).

Forest succession on lands that have been converted to non-forest tends to proceed differently from natural forest openings or lands that have been cut but not converted. Land that has been converted to non-forest uses tends to be depleted in organic matter and have suffered alterations of soil organic properties and have altered rates of organic matter decomposition and biomass accumulation (Aide *et al.* 1996). The species that dominate this type of secondary succession are often different from those that dominate natural gaps and cutover sites (Greig-Smith 1952 a, b, Uhl *et al.* 1988, Parrotta *et al.* 1997, Mesquita 2000, Mesquita *et al.* 2001). Two key elements can account for these differences – the fact that forest conversion (but not cutting alone) eliminates rootstocks and seedling banks (Ewel 1980, Murphy and Lugo 1986b, Corlett 1994,

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Molina Colón 1998, Boucher *et al.* 2000), and the fact that some pioneer species appear to inhibit the regeneration of primary forest species (Sim *et al.* 1992, Mesquita *et al.* 2001). In addition, the duration and intensity of use influences the pattern of succession (Hughes *et al.* 1999).

In Guánica Forest, Molina Colón (1998) found a distinct difference between areas that had been used for agriculture, housing and a baseball diamond, and forest land cut-over for charcoal production; in the 53 years since the villagers were relocated, the sites that had been used for charcoal production were indistinguishable from uncut forest in terms of species richness and basal area, while the other sites supported a species-poor community dominated by *Leucaena leucocephala* (Lam) de Wit. In St. John, U.S. Virgin Islands, Ray and colleagues (Ray 1993, Ray and Brown 1995) found that a 33-year-old abandoned pasture supported a species-poor community dominated by *L. leucocephala*, while a 50-year-old site supported a far richer community dominated by *Bourreria succulenta* Jacq. Similar successional patterns have been observed on abandoned agricultural land in the Dominican Republic (Roth 1999) and in Jalisco, Mexico (Burgos and Maass in review). Roth (1999) found that as much as 29 years after the cessation of agricultural activity, dry forests in Jacquí Picado in the Dominican Republic supported species-poor forests dominated by one native and two exotic leguminous trees, while (Burgos and Maass in review) found a similar situation in Mexico where 25-year-old abandoned agricultural land was dominated by one of two exotic legumes (which differed according to topographic location).

Castilleja (1991) found that, while there was enough light for seed germination below the forest canopy in Guánica Forest, and that seedling germination correlated inversel

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inversely with canopy cover, seedling survival through the dry season was dependent on dry season canopy cover. Similarly, Ray (1993) found that out-planted seedlings survived better below shade cloth in St. John, U.S. Virgin Islands. In addition, McLaren and McDonald (in press) found that dry forest seedlings grew best under light shade but that they survived best under heavy shade. As a consequence, it seems reasonable to assume that one of the factors related to the failure of *L. leucocephala* forests to accrete species richness is a consequence of the fact that seedling survivorship through the dry season is low under its fairly open deciduous canopy, although the fact that *L. leucocephala* is dry-fruited (and thus, unattractive to frugivorous birds and bats) may substantially reduce seed inputs.

Objectives

The objectives of the study were:

1) To quantify the current extent of forest cover in the dry forest zone in southwestern Puerto Rico;
2) To examine the drivers of land-use change in the period 1936-1993 as they pertain to the maintenance of forest cover in the dry forest zone;
3) To quantify the spatial patterns of forest cover from the perspective of connectivity across the landscape and identify gaps in the overall network of dry forest fragments;
4) To describe the historical dynamics of a subset of dry forest fragments that were the focus of a detailed study of their plant community structure and their role in the conservation of the dry forest biota (see Chapters 4-7).

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5) To determine whether the fragments support a species-rich native forest community or whether they are depauperate stands dominated by weedy exotic species;
6) To determine whether the basal areas and stem densities of the fragments are comparable with those found in Guánica Forest;
7) To determine whether distinct assemblages can be delineated on the basis of their plant species composition;
8) To evaluate the degree of nestedness present in the assemblage of dry forest fragments.
9) To explore the relationship between plant species richness and area in studied dry forest fragments;
10) To compare the effectiveness of a power function (Arrhenius equation) and a sigmoid function (the $\mathrm{Hill}_{\mathrm{Slope}}$ equation) as suggested by Lomolino (2000) in explaining the relationship between species richness and area;
11) To investigate the relationship between the per plot species richness ("species density" *sensu* Whittaker *et al.*, 2001) and total species richness in studied dry forest fragments.
12) To determine whether there is a correlation between abundance of species in the reference community (Guánica Forest) and their geographic range;
13) To determine whether there is a relationship between local abundance in Guánica Forest and frequency in sample plots within Guánica Forest;

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14) To determine whether there is a relationship between local abundance of plant species within Guánica Forest and the number of fragments within which a species occurs;

15) To determine whether there are differences in the distribution of species that are locally abundant in Guánica Forest and species present in most of the fragments in terms of the factors which determine of their presence in fragments of differing species richness and history;

16) To determine whether there are differences in seed size among fragments with different disturbance histories;

17) To determine whether there is a difference in the abundance of exotic species among fragments with different disturbance histories.

18) To develop methods to determine the conservation value of Puerto Rican dry forest fragments;

19) To evaluate the conservation potential of the studied dry forest fragments;

20) To designate and evaluate indicators of high quality dry forest fragments that can be used to prioritize conservation decisions.

Outline of the Study

The overall goal of this project was to expand knowledge of Puerto Rican dry forest from Guánica Forest, the largest intact patch of dry forest, to the array of fragments across the dry forest zone in southwestern Puerto Rico. To properly understand this dry forest system, it was useful to consider it at a variety of scales from species to the landscape level. The problem of managing this landscape to conserve the dry forest system

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system in Puerto Rico requires a multi-scale approach. Studies that attempt to make predictions about the biology of a system only on the basis of remotely sensed land-cover data usually attribute an unrealistic level of generality and predictive power to simple rules like species-area curves. While useful, such studies do not provide the multi-scale data needed for realistic conservation and management of fragmented tropical landscapes.

In order to provide the multi-scale data needed a group of 39 forest fragments were studied. The fragments ranged in size from 6×10^{-3} ha to 1372 ha and had experienced a wide range of disturbance types. In the absence of undisturbed, unfragmented examples of dry forest in Puerto Rico, Guánica Forest was chosen as the reference community against which the plant communities in the fragments were compared.

Land-cover dynamics in the dry forest zone of southwestern Puerto Rico were examined over the period 1936-1993. Forest and community structure of dry forest fragments were documented and the patterns of species distribution across the landscape were used to designate indicators of high-quality fragments.

The structure of the dissertation is as follows:

Chapter 1: Introduction (this chapter)

This chapter supplies background information on the impacts of habitat fragmentation on dry forests, and introduces the overall project.

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Chapter 2: Methods

This chapter introduces the study region and outlines the methods of data collection used in the study.

Chapter 3: Landscape Change and the Landscape Ecology of the Dry Forest Zone of Southwestern Puerto Rico

This chapter addresses the changes in land-use since 1936 as they pertain to this study, and supplies detailed histories of the 39 forest fragments that were the focus of the remainder of the study.

Chapter 4: Community Structure of Puerto Rican Dry Forests

This chapter describes the forest structure in a series of dry forest fragments, and groups them on the basis of plant species composition.

Chapter 5: Species-Area Relationships of Puerto Rican Plant Species in a Fragmented Landscape

This chapter examines the species-area relationships within and among the suite of studied forest fragments.

Chapter 6: Plant Species Responses to Long-term Fragmentation in Puerto Rican Dry Forest Landscape

This chapter looks at the distribution of plant species among the forest fragments and examines the factors that may be the drivers of these patterns.

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Chapter 7: The Conservation Potential of Forest Fragments on a Dry Tropical Landscape

This chapter evaluates the conservation potential of the forest fragments and designates species that can serve as indicators of fragments with high conservation potential.

Chapter 8: Conclusions and Recommendations

This chapter connects the whole work and seeks to make recommendations as to how this landscape may be managed for the conservation of native plant diversity.

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CHAPTER 2: METHODS

Study Region

This study was carried out in the western half of the dry forest life zone (*sensu* Holdridge 1967) of southwest Puerto Rico as delineated by Ewel and Whitmore (1973), a coastal strip between approximately 18°N 66° 35'W and 18°N 67° 12'W (Figure 2.1). All studied fragments were located west of the city of Ponce within a few kilometers of the southern coast of the island. The study area was located on the lee side of the island, in the rain shadow of the Cordillera Central and was classified as subtropical dry forest (*sensu* Holdridge 1967) by Ewel and Whitmore (1973).

The climate is seasonal with most rainfall occurring between August and November (Figure 2.2). Precipitation varies between 600 and 1000 mm annually (Ewel and Whitmore 1973). Climate Diagrams (Walter and Lieth 1967) based on the 1971-2000 monthly climate normals (National Oceanic and Atmospheric Administration 2001) were constructed for nine sites in and around the study area (Figures 2.1, 2.2).

On average, Puerto Rico experiences one hurricane every eight years (Quiñones 1992) but return rates on the south coast are about one every twenty-five years (Van Bloem *et al.* in press). While 37 hurricanes have hit Puerto Rico between 1700 and 1999, the eyes of only 12 of these came near the dry forest zone (Van Bloem *et al.* in press).

The dry forest life zone of southwestern Puerto Rico consists of alluvial valleys scattered among low hills. South out of the Cordillera Central there is a sudden onset of dryness. The green hills are replaced by faded yellow grasslands.

The forests are short in stature and the trees are multi-stemmed. Many of the trees are dry-season deciduous (Murphy and Lugo 1986); they drop their leaves in the dry season

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season as a means of water conservation. Dry-season deciduous trees are, for the most part, facultatively deciduous – the drier the year, the more pronounced the degree of deciduousness (see Medina *et al.* 1990, Eamus 1999, for discussion of the relationship between evergreenness and deciduousness in tropical dry forests). As a consequence of their short stature and multi-stemmed growth form, forests tend to form dense, almost impenetrable thickets consisting of a mass of thorny trunks, spiny lianas and patches of cacti. Large areas of successional vegetation dominated by *Leucaena leucocephala* and *Prosopis pallida* (H. & B. ex Willd.) HBK are also characteristic of the landscape.

Site Selection

Aerial photographs (1:33 000 color-infrared photographs December 1993), obtained from the United States Geological Survey, Eros Data Center, Sioux Falls, South Dakota, were used to locate, classify and map forest fragments across the dry forest life zone of southern Puerto Rico.

All potentially suitable fragments were identified using these aerial photographs and a subset of those was randomly selected for study. Access to these sites and actual conditions were determined by ground surveys. Sites that appeared to be forested on aerial photographs but which were actually wooded pasture were discarded. The original study design (Murphy and Burton 1993) envisioned dividing the dry forest zone into four

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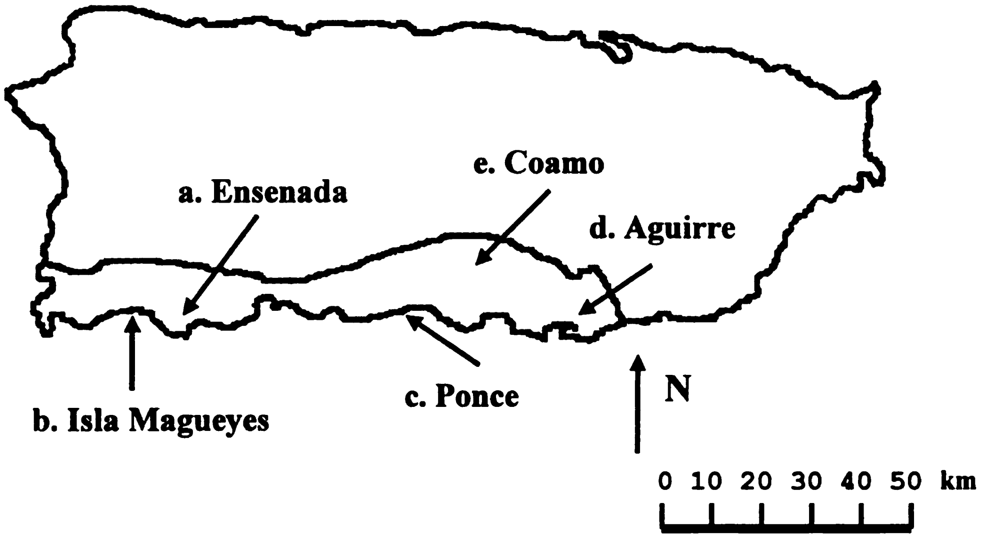

Figure 2.1. Map of Puerto Rico showing the dry forest zone (after Ewel and Whitmore 1973) and the approximate locations of weather stations used to construct Climate Diagrams. Letters refer to the order of the Climate Diagrams in Figure 2.2.

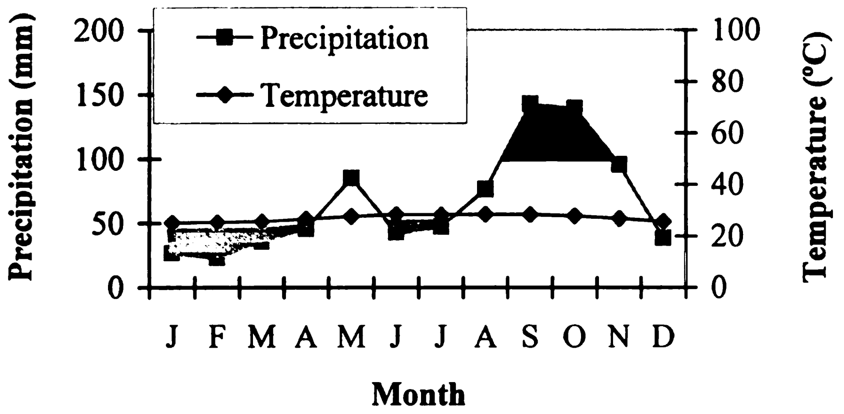

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Figure 2.2: Climate Diagrams (Walter and Lieth 1967) for the dry forest life zone in Puerto Rico based on NOAA 1971-2000 climate normals. Heavy shading areas (rainfall >100 mm mo^{-1}) represent water excess, while light shading represent water deficits.


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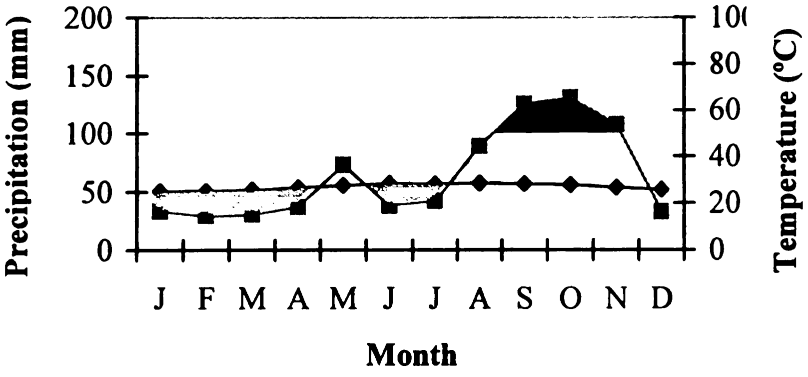

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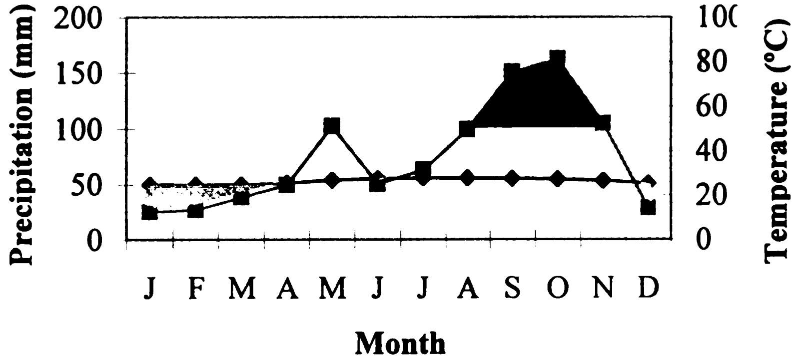

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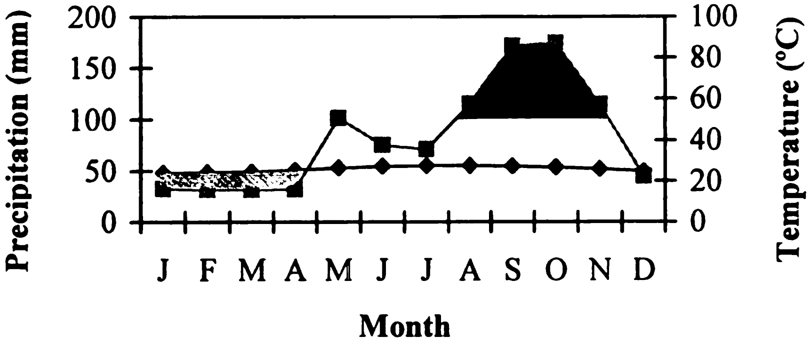

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Figure 2.2: (continued).

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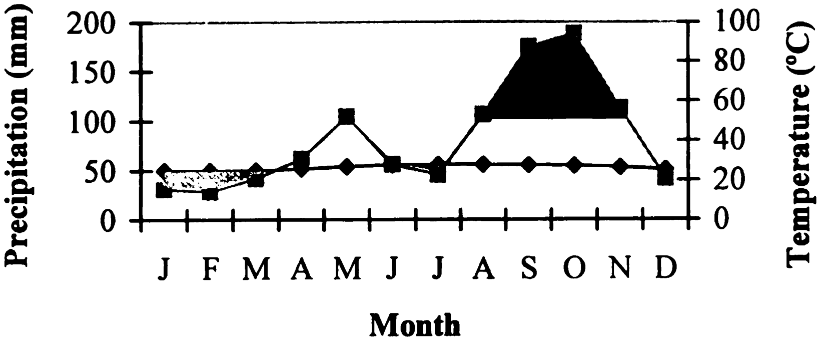

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Figure 2.2: (continued).

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geographic quadrants (northeast, southeast, southwest and northwest) with study sites evenly distributed among the four quadrants. The distribution of forest fragments (as determined from the aerial photographs) made the design impractical. Most forest fragments were concentrated in the southwestern quadrant. The flat land in the Lajas Valley (northwestern quadrant) and the areas east of the town of Ponce had little forest cover. In addition, the area between Ponce and Guayanilla provided few suitable sites as the area forms a large continuous patch of secondary dry forest without definable fragments.

A total of 39 fragments, ranging in size from 0.006-1392 ha were fully inventoried (Figure 2.3). Data were also collected from two other sites (Sites 3 and 41), but they were not fully inventoried. In one case the site was accessible when initially studied in 1996 but not in 1997 (Site 3, Figure 2.3). In the other case, the sampled "fragment" (Site 41) was later shown to be part of a much larger block of forest.

Existing forest fragments formed a continuum of sizes, slopes and aspects; many sites included more than one well-defined 'aspect'. In addition, the sites had variable disturbance histories – several were mosaics of patches with different histories – and the feasibility of many standardized comparisons among classes was limited. When selecting fragments, no attempt was made to control for the magnitude or recentness of past disturbance except that active pasture sites supporting monodominant stands of *Prosopis pallida* (an exotic leguminous tree) were excluded.

Reference plots within Guánica Forest were selected through discussion with the Park Manager, Miguel Canals Mora. Semi-evergreen and Deciduous plots were located

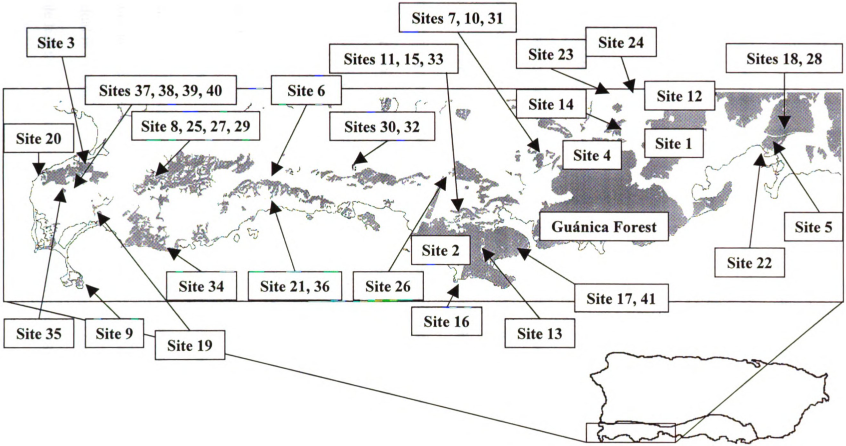

Figure 2.3: The location of studied forest fragments in the dry forest life zone of southwestern Puerto Rico. For details of the construction of the base map see Chapter 2. Approximate scale 1: 200 000. Inset map of Puerto Rico showing the dry forest zone (after Ewel and Whitmore, 1973) and the area from which the detailed map was selected.

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in areas that supported closed forest cover in 1936 (based on the maps of Vélez Rodriguez 1995a).

The location of each studied forest fragment was recorded using a Geographic Positioning System by staff of the USDA Forest Service International Institute of Tropical Forestry at Rio Piedras, Puerto Rico to facilitate the use of these sites in future studies.

Data Collection

Three separate plot-based methods (Table 2.1) and one plotless method were used to characterize the plant community of the sites. A variable number of circular plots (25 m^2 in area) were used to collect data on the identity and abundance of plant species within each fragment. Initially the height, species, and height of first branching were recorded for each individual over 0.5 m tall; the diameter at breast height (dbh; recorded at a height of 1.5 m) was recorded for each stem with a dbh of 1 cm or greater. The identity of any vines climbing these individuals and any epiphytes and the heights at which they were present were also recorded. Species less than 0.5 m tall were identified and abundances were recorded, by species.

To streamline data collection, these methods were later modified. A variable number of 25 m^2 circular plots were used in each site to record the species present, and the abundance of each species in each plot. Canopy height and the height of the tallest individual in each plot were also recorded. Belt transects (generally 2 m wide and of variable length) were used to collect data on the forest structure. The location and

Table 2.1: *Sampling design - the measurements collected for each of the three sampling designs used to study dry forest fragments and reference plots in Guanica Forest, southwestern Puerto Rico.*

Table 2.1: Sampling design – the measurements collected for each of the three sampling designs used to study dry forest fragments and reference plots in Guánica Forest, southwestern Puerto Rico.

25 m^2 Circular Plot - Original	25 m^2 Circular Plot - Modified	Belt Transect
Identity[a] of each individual over 0.5 m tall	Tally[b] of all individuals, by species	Identity[a] of each individual with a stem ≥ 1 cm dbh
Tally[b] of all individuals under 0.5 m tall, by species	Canopy height	Diameter, each stem ≥ 1 cm dbh, by individual
Height of first branching, all individuals over 0.5 m tall	Height of the tallest individual rooted within the plot	Identity[a] of vines ≥ 1 cm dbh, and identity of host trees
Diameter, each stem ≥ 1 cm dbh, by individual		
Identity[a] of vines climbing each individual, by species		
Identity[a] and height of epiphytes on each individual		

[a] Each individual was given a unique identifier, and the species to which it belonged was recorded

[b] The total number of individuals present in the plot was recorded for each species present.

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species of each tree with at least one stem ≥ 1 cm dbh were recorded. The dbh of each stem ≥ 1 cm was recorded for each of these trees. See Table 2.2 for a summary of the data collected at each studied fragment and in the reference plots in Guánica Forest.

The plot-based methods did not record every species in a fragment. To expand the species lists, 'site walks' were undertaken. Each fragment was searched as thoroughly as possible (given the limitations of time) and all new species encountered were recorded. A system of diminishing returns was used as a means of estimating the completeness of the search. If one hour of search time failed to record any additional species, a fragment or portion of a fragment was considered to have been adequately searched. Small fragments were completely searched. In larger fragments attempts were made to search each major feature of the site (*e.g.*, each major slope and each valley).

Different methods were used in several fragments (Table 2.2). In Sites 37-40 (the four smallest fragments) the entire fragment was treated as a single plot and the height, species, and height of first branching were recorded for each individual over 0.5 m tall and the dbh was recorded for each stem with a dbh of 1 cm or greater. Species less than 0.5 m tall were identified and abundances were recorded, by species. No plot-based sampling was done in Sites 31 and 32; species lists for the sites were compiled using a 'site walk'. No overall species list was compiled for Site 3 because access problems were encountered in 1997, or for Site 41 because it turned out not to be a fragment. Overall species lists were not compiled for the reference sites within Guánica Forest. Table 2.3 presents an overall summary of the data collected for each fragment.

Unknown plants were given field codes. Voucher specimens were collected for subsequent identification. Exceptions were made in the case of species thought to be rare

Table 2.2: *A summary of the sampling design employed for dry forest fragments and reference plots in Guánica Forest, southwestern Puerto Rico.*

Table 2.2: A summary of the sampling design employed for dry forest fragments and reference plots in Guánica Forest, southwestern Puerto Rico.

Site	Area	No. of 25 m^2 plots (structure + species)	No. of 25 m^2 plots (species only)	Area of belt transects, m^2 (no. of transects)	Total Area (species), m^2	Total Area (structure), m^2
1	1372	16	--	--	400	400
2	770	--	22	250 (5)	550	250
3	45	10	--	--	250	250
4	125	--	20	775 (7)	500	775
5	101	6	8	150 (3)	350	300
6	64	--	20	300 (3)	500	300
7	33	8	7	50 (1)	375	250
8	7	--	11	300 (3)	275	300
9	5.9	5	2	--	175	125
10	5.1	6	3	--	225	150
11	2.6	8	7	--	375	200
12	3	--	15	234 (3)	375	234
13	2	7	--	--	175	175
14	6	8	--	--	200	200
15	3.7	5	7	100 (1)	300	225
16	3.3	--	12	300 (3)	300	300
17	6.3	6	3	--	225	150
18	1.5	7	--	--	175	175
19	1.5	--	17	200 (2)	425	200
20	1.5	--	9	200 (2)	225	200
21	1.2	--	14	150 (2)	350	150
22	1.2	7	3	--	250	175
23	1	--	8	100 (2)	200	100
24	1	4	6	--	250	100
25	2.4	--	12	70 (1)	300	70

Table 2.2 *(continued).*

Site

Table 2.2 (continued).

Site	Area	No. of 25 m^2 plots (structure + species)	No. of 25 m^2 plots (species only)	Area of belt transects, m^2 (no. of transects)	Total Area (species), m^2	Total Area (structure), m^2
26	1	--	8	238 (4)	200	238
27	0.4	6	5	--	275	150
28	0.8	--	10	250 (2)	250	250
29	0.2	3	--	--	75	75
30	0.2	--	8	224 (2)	200	224
31	0.11	--	‡	--	--	--
32	0.1	--	‡	--	--	--
33	0.09	4	--	--	100	100
34	0.07	--	10	350 (3)	250	350
35	0.07	--	5	109 (2)	125	109
36	0.04	--	6	92 (2)	150	92
37	0.02	†	--	--	200	200
38	0.01	†	--	--	100	100
39	0.01	†	--	--	100	100
40	0.006	†	--	--	60	60
41	*	6	--	--	150	150
Guánica Forest	4000	--	19	910 (4)	475	910

* This was not a well-defined fragment; no estimate of area was made.

† These entire sites were sampled as single plots and structural and species data were collected for the entire site.

‡ Species lists were compiled at these sites, but not quantitative sampling was carried out.

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Table 2.3: A summary of the data collected for dry forest fragments and reference plots in Guánica Forest, southwestern Puerto Rico (see text for details).

Site	Structure	Abundance	Overall Species List
1	+	+	+
2	+	+	+
3	+	+	-
4	+	+	+
5	+	+	+
6	+	+	+
7	+	+	+
8	+	+	+
9	+	+	+
10	+	+	+
11	+	+	+
12	+	+	+
13	+	+	+
14	+	+	+
15	+	+	+
16	+	+	+
17	+	+	+
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26	+	+	+
27	+	+	+
28	+	+	+
29	+	+	+
30	+	+	+
31	-	-	+
32	-	-	+
33	+	+	+
34	+	+	+
35	+	+	+
36	+	+	+
37	+	+	+
38	+	+	+
39	+	+	+
40	+	+	+
41	+	+	-
Reference Plots	+	+	-

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or endangered; in such cases field notes were used for later identification. Newly encountered species represented by single individuals were not collected except in the case of larger woody plants where it appeared that collections would not adversely affect the survival of the plant. Voucher specimens were prepared using a plant press and were dried using a field dryer constructed using a 100-watt light bulb. Voucher specimens were deposited at the Beal-Darlington Herbarium at Michigan State University. Species nomenclature follows (Liogier 1985, 1988, 1994, 1995, 1997) except where otherwise stated.

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CHAPTER 3: LANDSCAPE CHANGE AND THE LANDSCAPE ECOLOGY OF THE DRY FOREST ZONE OF SOUTHWESTERN PUERTO RICO

Introduction

The survival of native species on a fragmented landscape requires the preservation of adequate amounts of habitat. The dynamics of this habitat profoundly affects species conservation. Dry forests are resilient after cutting (*e.g.*, for firewood or charcoal production; Ewel 1980, Dunevitz 1985, Murphy *et al.* 1995, Molina Colón 1998) but are slow to recover from prolonged agriculture (Ray 1993, Molina Colón 1998, Roth 1999, Burgos and Maass in press). Most of the native tree species are slow to recolonize areas from which rootstocks have been eliminated (Molina Colón 1998). As a consequence of this, second growth forest can be almost indistinguishable from uncut forest after fifty years, or can have a radically different species composition depending on whether it was used for charcoal production or row crops (Molina Colón 1998, Erickson *et al.* 2002; see Chapter 4).

The dry forests of Puerto Rico have a long history of human impacts. As early as 1879 local Spanish officials expressed concerns about the quality of surviving wood resources in the southern part of the island (Wadsworth 1950). The early twentieth century saw the expansion of sugar cane cultivation and the demise of the coffee industry following the American annexation of the island (Dietz 1986, Santiago 1992). This led to a major shift in the rural population away from the mountainous interior into the coastal lowlands. Between 1899 and 1910, while the population of Puerto Rico grew by 17.3%, the population of Guánica Municipality grew by 121.4% (Dietz 1986). This increase in

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population density would have increased the local demand for forest products, especially for charcoal, the main fuel used for cooking (Murphy 1916). Sugar production also contributed to the degradation of the forest resource. In addition to competing directly with forest as a land use, sugar refining put heavy demands on remaining forest land; Murphy (1916) reported that the sugar refineries were major consumers of fuel wood. Seven sugar refineries were located in the southwestern portion of the island in the later 1920s including Central San Francisco, the largest sugar refinery in the island (Chardon 1927).

Puerto Rico is likely to have been almost entirely forested at the time of European contact in 1493 (Wadsworth 1950). By the late 1940s forest cover had been reduced to about 7% of the island (Birdsey and Weaver 1982, Birdsey and Weaver 1987). A shift in government policy from the 1940s onward changed the economy from one based on agriculture to one based on manufacturing industries. This was coupled with increased emigration to the U.S. mainland in the postwar period. These changes reduced dependence on the land and absorbed labor surpluses (Dietz 1986, Santiago 1992). This resulted in reforestation, as abandoned land returned to forest. Between 1948 and 1990 reforestation averaged 0.63% of the island per annum (Rudel *et al.* 2000) and forest cover now stands at about 35% (Birdsey and Weaver 1987, FAO 1998). Puerto Rico has experienced the highest rates of reforestation in the world in the postwar period (Rudel *et al.* 2000). The countries with the next highest rates of reforestation in this period were Germany and Austria, whose rates of 0.25% per annum (Rudel *et al.* 2000) were considerably lower than that of Puerto Rico.

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Most of the forest land that survived the peak era of deforestation was located in the Luquillo Mountains in the northeast of the island or in one of several small tracts in the Cordillera Central (Wadsworth 1950, Brash 1978, Figueroa Colon 1996). In southwestern Puerto Rico, forest cover was concentrated around Guánica Forest, a tract of dry forest that was set aside in 1919 as a 2079-ha reserve and subsequently expanded to its present 4000 ha. Gleason and Cook (1926) also referred to a "relict tract" of dry forest near Tallaboa. Figueroa Colon (1996) considered the Sierra Bermeja, a range of hills to the east of Guánica Forest, to be another important repository of plant diversity during this period. The Sierra Bermeja supports six of the 13 federally listed endangered species potentially present in the areas (see Chapter 7). Two of these species are endemic to the summit of a single hill, the Cerro Mariquita. This makes the area richer in endangered species than Guánica Forest (which supports five endangered species, two of which are endemic to the reserve).

Most of the reforestation has occurred in the mountainous interior of the island (Rudel *et al.* 2000) but Lugo *et al.* (1996) recorded extensive reforestation in the lowland dry forest zone in the vicinity of Guánica Forest. Rudel *et al.* (2000) discussed two models to explain recovery. One model, the "forest transition hypothesis" posits the change to be driven by reduced demands on the land as a consequence of industrialization. In more industrialized societies workers are drawn to jobs in the manufacturing and service sectors and away from agriculture. With more cash income and less time available to spend on the land (Preston 1989, Rudel *et al.* 2002), goods and services previously obtained from forest fragments are now purchased from other sources. Thus, the pressure on the land decreases. Their other model, the "special relat

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relationship hypothesis", suggests that Puerto Rico's special relationship with the U.S.A. increased the cost of labor through the provision of Federal Assistance programs and reduced the supply through emigration to the mainland. This increase in the cost of labor made agriculture economically unviable and thus led to the abandonment of agricultural land, which was then allowed to revert to forest.

Historical land use and current patterns of forest cover are likely to play an important role in determining the distribution of plant species across the landscape. Understanding these land-use patterns is important in interpreting species patterns.

Objectives

1) To quantify the current extent of forest cover in the dry forest zone in southwestern Puerto Rico;
2) To examine the drivers of land-use change in the period 1936-1993 as they pertain to the maintenance of forest cover in the dry forest zone;
3) To quantify the spatial patterns of forest cover from the perspective of connectivity across the landscape and identify gaps in the overall network of dry forest fragments;
4) To describe the historical dynamics of a subset of dry forest fragments that were the focus of a detailed study of plant community structure and their role in the conservation of the dry forest biota (see Chapters 4 – 7).

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Methods

Landscape Characterization

Aerial photographs (1:33 000 color-infrared photographs December 1993), obtained from the United States Geological Survey, Eros Data Center, Sioux Falls, South Dakota, were used to locate, classify and map forest fragments across the dry forest life zone of southern Puerto Rico. Aerial photograph coverage amounted to 73 000 ha of the dry forest life zone (about 60% of the total dry forest life zone of the island of Puerto Rico; Ewel and Whitmore 1973).

Landscape elements dominated by woody vegetation were classified as either 'Closed Forest' or 'Open Forest', based on the amount of ground cover that was visible between tree crowns, using FAO criteria for the classification of vegetation (FAO 1993). Fragments with more than 50% of the ground visible were classified as Open Forest, while those with less ground visible were classified as Closed Forest.

Forest fragments were mapped using acetate overlays. The entire area was divided into 15 blocks to facilitate data collection. Each block was approximately 7 km wide (east to west) and a variable depth inland (north to south) from the coast, depending on the width of the dry forest zone at that point. Fragment areas were estimated using squared paper and were grouped into five size classes (< 5 ha, 5-10 ha, 10-50 ha, 50-100 ha and > 100 ha). The forest cover in the entire study region and in each of the 15 blocks was calculated.

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Landscape Change

Land cover data were collected from a series of six published land cover maps spanning a 53-year time period (Vélez Rodriguez 1995a, b, c, d, e, f) covering two USGS Quadrangles surrounding Guánica Forest Biosphere Reserve, Puerto Rico. The published maps were prepared using traditional photo-interpretive methods (Lugo *et al.* 1996). Time series land cover data were collected by overlaying a 2 cm x 2 cm grid on each map and recording the land cover class present at each point in the grid. Efforts were made to register the grid in the same manner on each map to ensure continuous monitoring of the same set of points through time. A total of 529 data points were collected from each map. Land cover classification followed those used in the maps (Anderson *et al.* 1976) except that the three wetland classes and the three barren ground cover classes were aggregated into a single wetland and a single barren ground class respectively.

Transition probabilities (the probability that a point would 'transition' from one cover class to another or that it would remain in the same cover class) were calculated for each point between each pair of maps. Thus, the probability of change from one cover type to another was not calculated for the whole area, but instead was calculated for individual points.

Dynamics of Focal Fragments

A chronosequence of aerial photographs was used to assess changes in forest cover and land-use in and around a subset of fragments that were the subject of a more detailed study of plant community structure and conservation potential (see Chapters 2, 4 – 7). Study-sites were selected as outlined in Chapter 2. Aerial photographs from 1936

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(1:18 000 black and white photographs, obtained from the Oficina de Fotogrametria, Autoridad de Carreteras y Transportacion, San Juan, Puerto Rico), 1963 (1:20 000 black and white photographs, obtained from the Oficina de Fotogrametria, Autoridad de Carreteras y Transportacion, San Juan, Puerto Rico), and 1993 (1:33 000 color-infrared photographs December 1993, obtained from the United States Geological Survey, Eros Data Center, Sioux Falls, South Dakota) were used to assess change. Site histories were constructed for each of the fragments with the exception of one that was outside of the area for which aerial photo-coverage was obtained. Fragments were classified on the basis on the proportion of the site that was 'old growth' – *i.e.*, areas that had supported forest cover continuously since 1936. Each fragment was classified as Relict (> 75% 'old growth'), Mixed (25-75% old growth) or Regrowth (< 25% old growth). Attempts were made to ascertain the causes of decreases in fragment size. When patch size decreased, land-use in the area lost from the fragment was used to classify the cause of the decline in patch size. These changes were classified as i) Agricultural or ii) Urban, Industrial or Infrastructural. On-the-ground observations were used to describe changes that had occurred during and after the fragment inventories (see Chapter 2) were carried out.

Fragment Networks and Connectivity

Unrectified aerial photographs (1: 33 000 color-infrared photographs December 1993), obtained from the United States Geological Survey, Eros Data Center, Sioux Falls, South Dakota were scanned and a photomosaic of the study area was constructed using Photoshop 5.5 (Adobe Systems, 1999). A forest cover map was constructed by tracing the areas of forest cover on this image. To assess potential connectivity between fra

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fragment clusters, gaps between clusters greater than 500 m and greater than 1000 m were identified and recorded. These distances were selected based on da Silva *et al.* (1996), Lamb *et al.* (1997) and Graham (2001) – the smaller distance (500 m) represented a distance at which seed movement was thought to be unlikely (given the movement patterns of potential seed dispersers), while the larger distance (1000 m) represented a distance at which almost no seed movement was to be expected.

Results

Landscape Characterization

Forest cover stood at 23.2% in the dry forest zone in 1993 (Table 3.1); 18.0% of the forest cover was Closed Forest and 5.2% was Open Forest. Closed Forest was the dominant wooded land-cover category in 1993, covering more than three times the area occupied by Open Forest (Table 3.1). Forest cover peaked toward the middle of the dry forest zone, and decreased toward the eastern and western end. Closed-Forest cover varied across the landscape more than did Open Forest cover. Closed Forest cover ranged from 0.6 to 67.4% of the area of each block, while Open Forest ranged from 0.6 to 9.2% of each block (Figure 3.1). The city of Ponce, the second-largest city in Puerto Rico, was located in Block 10. The town of Guánica was located in Blocks 4 and 5.

Fifty-two percent of all fragments (322 fragments) were below 5 ha, and accounted for 4% of the total forest cover (Table 3.1). Three percent of all fragments (20 fragments) were over 100 ha, and these accounted for 63% of all forest cover (Table 3.1). The mean fragment size was 42.6 ha for Closed Forest fragments and 12.3 ha for Open

Table 3.1: *Distribution of forest cover (based on 1993 aerial photographs),* **by size class, in the dry forest zone, southwestern Puerto** *Rico. Column totals may not precisely match the values in the columns due to rounding*

Table 3.1: Distribution of forest cover (based on 1993 aerial photographs), by size class, in the dry forest zone, southwestern Puerto Rico. Column totals may not precisely match the values in the columns due to rounding.

	Closed Forest				Open Forest			
Fragment Size Class	No. of Fragments	Area (ha)	% of Total Forest Area	% of Life Zone	No. of Fragments	Area (ha)	% of Total Forest Area	% of Life Zone
< 5 ha	166	384	2.9	0.5	156	362	9.5	0.5
5-10 ha	43	294	2.2	0.4	72	517	13.5	0.7
10-50 ha	71	1616	12.3	2.2	66	1371	35.8	1.9
50-100 ha	14	961	7.3	1.3	12	784	20.5	1.1
> 100 ha	14	9878	75.2	13.5	6	793	20.7	1.1
Total	308	13133	100	18.0	312	3827	100	5.2

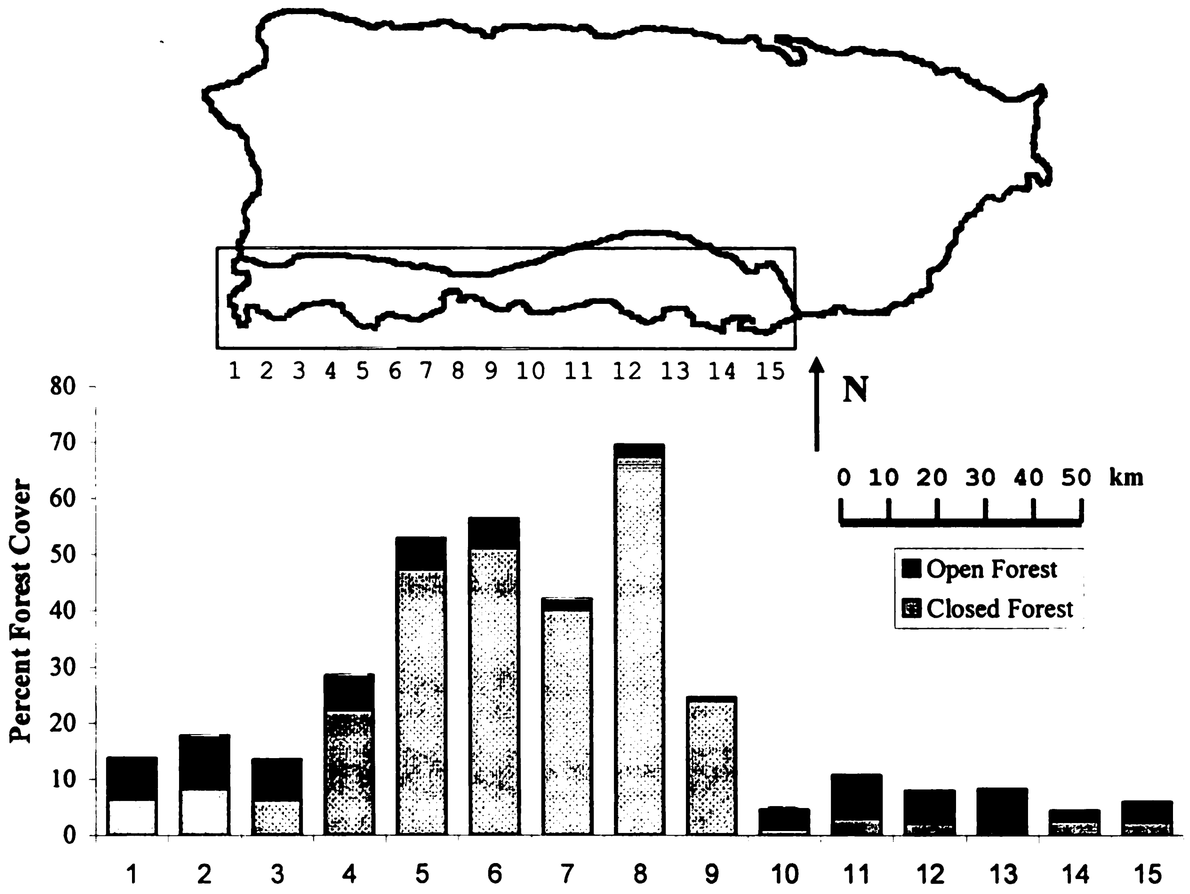

Figure 3.1: The distribution of forest cover from west to east in the dry forest zone, southwestern Puerto Rico. The boxed area on the map shows the area covered by the graph. Each block was approximately 7.5 km wide. See text for additional details. The scale refers to the map of Puerto Rico. The highlighted area in the south of the island lies within the dry forest life zone (*sensu* Holdridge 1967) as delineated by Ewel and Whitmore 1973).

Table 3.2: *Transition probabilities between Agriculture, Open Forest and Closed Forest in dry forest fragments of southwestern Puerto Rico in the period 1936-1989. Transitions are based on the probability of a point in a given land-cover class ending in the same or another land-use class between the named time periods.*

Transition†

Table 3.2: Transition probabilities between Agriculture, Open Forest and Closed Forest in dry forest fragments of southwestern Puerto Rico in the period 1936-1989. Transitions are based on the probability of a point in a given land-cover class ending in the same or another land-use class between the named time periods.

	Transition†								
	1 3	1 2	1 1	3 3	3 2	3 1	2 3	2 2	2 1
1936-50/51	0.09	0.05	0.81	0.77	0.17	0.02	0.60	0.36	0.03
1950/51-63	0.09	0.03	0.80	0.78	0.16	0.03	0.71	0.24	0.04
1963-71	0.06	0.05	0.84	0.83	0.09	0.05	0.77	0.14	0.08
1971-83	0.14	0.01	0.80	0.90	0.04	0.03	0.65	0.20	0.13
1983-89	0.06	0.30	0.62	0.90	0.07	0.01	0.70	0.25	0.05

† 1 1 – Agriculture to Agriculture
1 2 – Agriculture to Open Forest
1 3 – Agriculture to Closed Forest
2 1 – Open Forest to Agriculture
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Forest fragments. The median size of Closed Forest fragments was less than 5 ha while the median Open Forest fragment was approximately 5 ha.

Landscape Change

In two of the three classes considered (Agriculture and Closed Forest) the predominant transition was retention in the same class (Table 3.2), although it fell from over 0.8 to 0.52 for Agriculture in the 1983-1989 interval. The primary transition for Open Forest was to Closed Forest; retention was more prevalent than the transition from Open Forest to Agriculture.

In two of the land-cover classes (Agriculture and Closed Forest) retention was the most prevalent transition; this declined over time for Agriculture, but increased for Closed Forest.

Dynamics of Focal Fragments

The dry forest fragments that were the focus of detailed study ranged in size from 6×10^{-3} ha to 1372 ha in 1993. Twenty-three of the studied fragments (59%) have maintained some amount of forest cover throughout the 1936-1989 period. Eighty-nine percent of the total area occupied by the fragments was 'old growth' (*i.e.*, had been forested continuously since 1936, although stems are likely to have been harvested for fence posts and charcoal production). Nineteen fragments were classified as Relict on the basis of being 75-100% 'old growth', three were classified as Mixed (25-75% 'old growth') and 17 fragments were classified as Regrowth (0-25% 'old growth').

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Twenty-three of the studied forest fragments increased in size, 14 decreased in size and two remained about the same size between 1936 and 1993 (Table 3.3). Of the 14 fragments that decreased in size, six fragments appear to have shrunk because of agricultural development, six appear to have shrunk as a consequence of urban, industrial or infrastructural development and two fragments appear to have declined in size as a consequence of both causes. Of the four fragments that were eliminated between 1995 and 1998, three were eliminated as a consequence of urban, industrial or infrastructural development and one was destroyed by fire. Five other fragments also decreased in size during the 1995-1997 interval (Table 3.3).

Fragment Networks and Connectivity

A total of nine clusters and eight major gaps were identified using a 500-m cut-off between fragment clusters (Table 3.4). Using a 1000-m cut-off only one gap was identified – the gap separating the forests on the Cabo Rojo peninsula from all other forest fragments (Figure 3.2).

Table 3.3: *History of studied dry forest fragments, southwestern Puerto Rico, in the period 1936-1993 with additional notes on changes in the period 1995-1998.*

Area	% Old	Net

Table 3.3: History of studied dry forest fragments, southwestern Puerto Rico, in the period 1936-1993 with additional notes on changes in the period 1995-1998.

Site	Area 1993	% Old Growth	Net Change	Status	Comments
1	1372	95	+/-	Relict	Largely unchanged in area since 1936, but the forest appears taller with a more closed canopy.
2	770	74	+	Mixed	A large forested block forms the core of this fragment, but about a quarter of this site is Regrowth forest largely dominated by *Leucaena leucocephala* and *Prosopis pallida.*
3	45	19	+	Regrowth	Forest cover here was restricted to north and west-facing slopes in 1936, but gradually expanded.
4	125	78	+	Relict	Large areas of agricultural land (about a quarter of the site) to the north and south of the site reverted to forest and combined with the 'old growth' core.
5	101	82	-	Relict	This site is a portion of a larger 1300-ha block of forested land, from which it was separated by road construction and by the development of a petrochemical complex. The western part of the site and some internal valleys were not forested in 1936, but reverted to forest by 1993.
6	64	76	+	Relict	Several distinct forest patches coalesced into the present forest fragment.
7	33	97	-	Relict	This site was part of a large block of forest that included Sites 10 and 31. Parts of this block were converted to pasture, while other parts were consumed by suburban development and road construction.
8	7	100	-	Relict	This site was originally contiguous with Site 27, but they were separated by the construction of a road.
9	5.9	93	+	Relict	While forest cover has expanded slightly, it has been fragmented by the expansion of trails through the forest.
10	5.1	57	+	Mixed	Originally part of the same block of forest as Sites 7 and 31, this fragment was isolated by road construction and the construction of houses. Almost half the fragment is abandoned agricultural land that has reverted to forest

Table 3.3 (continued).

Site	Area 1993	% Old Growth	Net Change	Status	Comments

Table 3.3 (continued).

Site	Area 1993	% Old Growth	Net Change	Status	Comments
11	2.6	100	-	Relict	This site was originally connected with Sites 15 and 33 in a larger site that gradually shrank and was fragmented. Attempts were made to convert this site to pasture, but this is not apparent from the chronosequence of aerial photographs
12	3	no data		--	Site is outside the coverage of the set of aerial photographs
13	2	100	+	Relict	This site was originally a wooded patch within a golf course. Although the golf course has been abandoned, the boundaries of the patch were still distinct in 1993.
14	6	100	-	Relict	Part of a larger forest patch prior to fragmentation of that patch.
15	3.7	100	-	Relict	Originally part of a larger forest fragment that included Sites 11 and 33.
16	3.3	100	-	Relict	Originally part of a larger area of forest that was isolated by the expansion of the town of Playa Santa.
17	6.3	100	+/-	Relict	
18	1.5	90	-	Relict	Part of a larger 1300-ha forest patch that included Sites 5 and 28. That patch was internally fragmented by a network of roads, creating this fragment.
19	1.5	0	+	Regrowth	Although a few scattered trees were present in the area in the 1936 aerial photographs, the present forest patch developed between 1963 and 1993.
20	1.5	0	+	Regrowth	Although this site was wooded in the 1936 aerial photographs, it was cleared between then and 1963; the present forest patch developed after 1963.
21	1.2	100	-	Relict	Originally connected by a small strip of forest to a larger patch, this site was isolated by the elimination of this strip.
22	1.2	0	+	Regrowth	Site was covered by short scrubby vegetation and 1936.
23	1	0	-	Regrowth	Forest cover only developed after 1963.

Table 3.3 (continued).

Site	Area 1993	% Old Growth	Net Change	Status	Comments

Table 3.3 (continued).

Site	Area 1993	% Old Growth	Net Change	Status	Comments
24	1	0	+	Regrowth	Not covered by the aerial photographs, but conversations with a resident revealed that the site had been pasture "a few" years before.
25	2.4	59	+	Mixed	A small patch of forest that expanded first into the adjacent ravine, and then into the intervening hillside.
26	1	0	+	Regrowth	Forest cover only developed after 1963.
27	0.4	100	-	Relict	Separated from Site 8 by the construction of a road between 1963 and 1993.
28	0.8	100	-	Relict	Originally part of a larger 1300-ha block that included Site 5 and 18. This site was isolated between 1963 and 1993.
29	0.2	0	+	Regrowth	This site was non-forest prior to the 1963-193 interval.
30	0.2	0	+	Regrowth	Low scrubby vegetation in 1936.
31	0.11	100	-	Relict	This site was connected to Site 7 until the 1963-1993 interval.
32	0.1	0	+	Regrowth	Low scrubby vegetation in 1936.
33	0.09	0	+	Regrowth	This site was originally part of the same patch of forest as Sites 11 and 15, but lacked forest cover in the 1963 aerial photographs. It was cleared again between July 1995 and January 1996.
34	0.07	0	+	Regrowth	A few scattered trees were present in 1963, but no real forest cover was present before the 1993 aerial photographs.
35	0.07	0	+	Regrowth	This site was treeless in the 1936 aerial photographs, but had developed into open woodland by 1963. The patch present in the 1993 aerial photographs was larger than what was present when the site was studied in 1996. The site was entirely cleared between May 1996 and May 1997.
36	0.04	100	-	Relict	This site was connected to a larger patch of forest by a narrow strip on trees in 1936, but was completely isolated by 1963. The patch burned in the 1997-1998 dry season.

Table 3.3 *(continued).*

Site	Area 1993	% Old Growth	Net Change	Status	Comments

Table 3.3 (continued).

Site	Area 1993	% Old Growth	Net Change	Status	Comments
37	0.02	0	+	Regrowth	This site is absent up to the 1963 aerial photographs.
38	0.01	0	+	Regrowth	This site is absent up to the 1963 aerial photographs.
39	0.01	0	+	Regrowth	This site is absent up to the 1963 aerial photographs.
40	0.006	0	+	Regrowth	This site is absent up to the 1963 aerial photographs.

Table 3.4: The characteristics of dry forest fragment clusters separated from each other by more than 500 m, southwestern Puerto Rico

Sites Included

Table 3.4: The characteristics of dry forest fragment clusters separated from each other by more than 500 m, southwestern Puerto Rico

Fragment Cluster	Characteristics	Sites Included
1	The western extent of a large block of forest that extends as far as the city of Ponce. No significant protected areas.	5, 18, 22, 28
2	Included the largest protected area (Guánica Forest) and several large towns (Guánica, Yauco, Guayanilla, Ensenada).	1, 2, 4, 7, 10, 11, 12, 13, 14, 15, 16, 17, 23, 24, 26, 31, 33, 41
3	Northwest of the town of Yauco; disturbed sites but they may be important because they lie between Guánica Forest and the Cordillera Central.	-
4	An inland strip of forest south of Carretera 16, mostly disturbed regrowth.	30, 32
5	A complex set of fragments including the Sierra Bermeja, abandoned pasture immediately south of them, and hill forests north of the town of La Parguera.	6, 8, 21, 25, 27, 29, 34, 36
6	Secondary forest around the Cabo Rojo National Wildlife Refuge.	19
7	Secondary forest on low hills between the towns of Boquerón and El Combate.	3, 20, 35, 37, 38, 39, 40
8	An area of abandoned pasture south of the El Combate area.	-
9	Morillos de Cabo Rojo: a small isolated area of forest at the southwestern extreme of Puerto Rico.	9

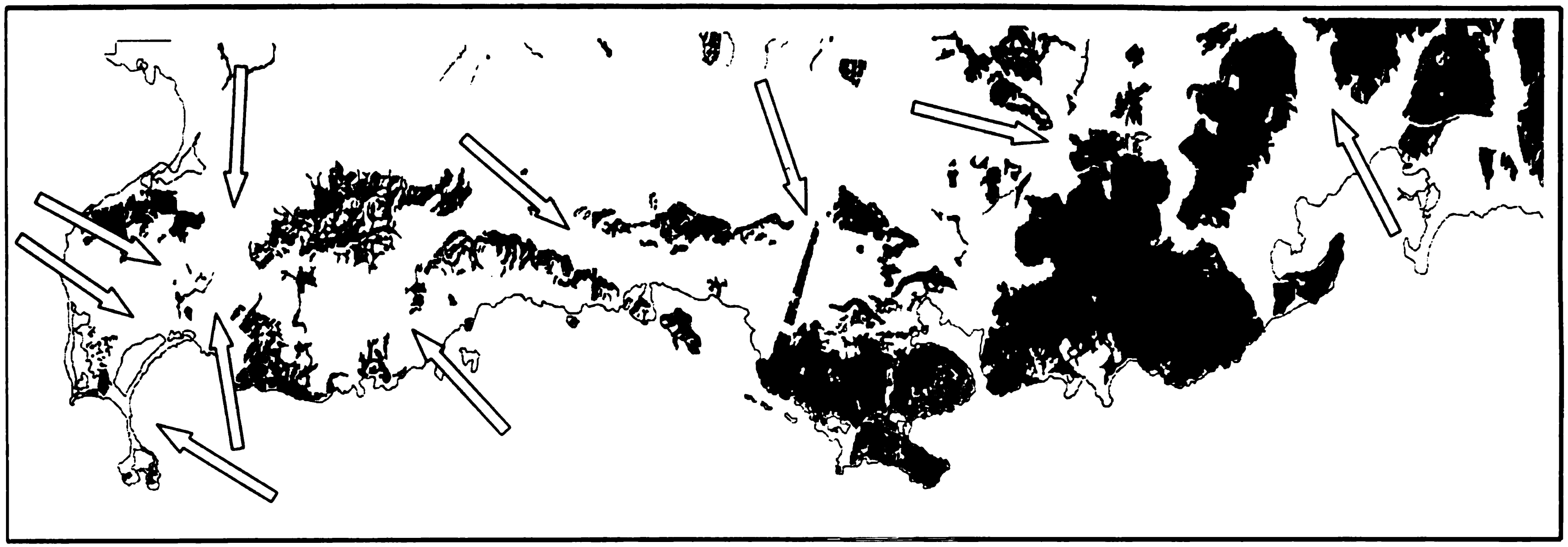

Figure 3.2: Map showing the extent of forest cover in the study region of southwestern Puerto Rico. Arrows indicate gaps of more than 500 m between clusters of fragments. Approximate scale 1:170 000.

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Discussion

Habitat destruction is one of the major causes of biodiversity loss (Wilson 2002). While some forest species are able to survive in a matrix of altered habitats, in general, forest species require forest habitat. While it is unlikely that the magnitude of forest recovery observed in Puerto Rico will be repeated in many other parts of the tropics, an understanding of the conditions that facilitated this recovery may help in the identification of other areas where reforestation is feasible. Understanding the drivers of this change can help to identify areas where reforestation is likely to succeed and areas where the prospects of success are poor. Rudel *et al.* (2000) identified other limited areas where a similar set of conditions exist, for example in parts of the Greater Antilles (Zweifler *et al.* 1994) and in the Andean region of South American (Rudel *et al.* 2002).

Forest Cover

At 23.2% forest cover (18.0% Closed Forest and 5.2% Open Forest), the dry forest zone is well below the overall estimate of 35% forest cover for Puerto Rico (FAO 1998). While there was relatively little forest cover east of the city of Ponce and west of the town of Guánica, forest cover between these towns was high, and included substantial areas that supported Open or Closed Forest even in the 1936 aerial photographs, including most of Guánica Forest. These areas of high forest cover are the core of the dry forest in Puerto Rico and are probably the key to the long-term survival of the dry forest biota.

Most dry forest fragments were small. Fragments smaller than 5 ha accounted for 54% of all Closed Forest fragments and 50% of all Open Forest fragments, but only 2.9%

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of the Closed Forest and 9.5% of the Open Forest cover. Fourteen Closed Forest fragments greater than 100 ha accounted for 4.5% of all Closed Forest fragments, but 75.2% of all Closed Forest cover.

Ranta *et al.* (1998) found 1839 forest fragments in a 2674 km^2 portion of the Brazilian Atlantic rainforest that ranged in size from 0.06 to 1539 ha and had an average size of 34 ha; this amounted to 0.69 fragments per hectare, a figure that was close to the density of 0.51 fragments per hectare observed in southwestern Puerto Rico. Forest cover in the Brazilian landscape was about the same as in southwestern Puerto Rico – 23% in both cases. Forty-eight percent of Brazilian fragments were smaller than 10 ha (versus 70% in Puerto Rico) while only 7 % were larger than 100 ha (as compared with 3% in southwestern Puerto Rico). While Ranta *et al.* (1998) considered the distribution of forest cover in Brazil to be a stable end state, the distribution of forest cover in Puerto Rico is probably still changing (as shown by changes observed between 1995 and 1998) – agriculture remains unprofitable (thus, likely to lead to increased forest abandonment) but forest cover is threatened by housing and resort development.

Large forest fragments are likely to support more species than small fragments (see Chapter 5). Large fragments are less likely to lose species after isolation than are small fragments (Hanski and Ovaskainen 2002). Laurance *et al.* (2002b) and Alvarez-Buylla *et al.* (1996) suggested that reserves in the mainland Neotropics should be on the order of hundreds of square kilometers; optimal reserve sizes for many continental species are likely to be larger than many Caribbean islands. Dry forests are less species rich (Murphy and Lugo 1986a), and thus less likely to have as many rare species (Hubbell 2001). As a consequence of this, the optimal size of conservation units is likely

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to be smaller for dry forests than for wetter ones. In addition, dry forests in the insular Caribbean are likely to carry lower genetic loads and to have smaller minimum viable population sizes (Lande 1995, Alvarez-Buylla *et al.* 1996) by virtue of the fact that they have evolved as relatively small populations. Fourteen Closed Forest fragments (comprising a total of almost 10000 ha) each exceeded 100 ha in size. Another 14 fragments were in the 50-100 ha range. If these can be protected from deforestation they may form a core area that can be managed for biodiversity conservation.

The conservation value of many of the small fragments is likely to be fairly low, especially for those that are primarily Regrowth (see Chapter 7). Nonetheless, fragments may support viable populations of certain species. For any such species these fragments may be valuable elements of the entire genetic diversity of the species (*e.g.*, Aldrich and Hamrick 1998, Aldrich *et al.* 1998). Many dry forest trees would fit the definition of resprouters (Kruger *et al.* 1997, Bond and Midgley 2001, Kruger and Midgley 2001), in which case the life span of an individual genet is likely to be very long. Such species are likely to have a long persistence time even in small fragments. The presence of small fragments may also reduce the gap between large areas of forest. This may reduce the movement cost (Graham 2001) for bats, birds and insects between fragments and thus increase the probability of gene flow among fragments.

Taken broadly, it seems reasonable that it should be possible to explain forest cover in economic terms (Kahn and McDonald 1997). Areas that remain under forest cover (and thus, by extension, areas that are allowed to revert to forest) are areas in which the marginal cost of converting the land to non-forest cover exceeds the post-conversion benefits derived from that land. Similarly, land is likely to be allowed to revert to forest co

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cover if the cost of maintaining it as non-forest exceeds the marginal benefit derived from the current land use. In this context, the findings of Ramos González (2001) are to be expected – with the collapse of the agricultural sector in Puerto Rico, former agricultural lands are likely to either become urbanized or to be allowed to revert to forest. This change has resulted in the observed pattern in which urban development has encroached up to the boundary of protected areas (as has also happened in the case of the community of La Luna and the city of Guánica which have grown right up to the border of Guánica Forest). Distance decay theory (Clark 1951, in Wickham *et al.* 2000) and retail gravity (Carrothers 1956, in Wickham *et al.* 2000) predict that distance from economic centers and the size of these centers are the principal determinants of land demand; for example, deforestation was greatest near major population centers in the Mexican state of Morelos (Trejo and Dirzo 2000). This would then predict that forest cover should be lower near urban centers and higher away from them. However, this explanation is likely to be most applicable either in actively developing frontiers or in old agricultural landscapes which have reverted to forest as a consequence of economic transitions and are, in effect, secondary frontiers.

The pattern observed in southwestern Puerto Rico was not in keeping with the latter hypothesis. Forest cover was high adjacent to the large towns (Ponce, Yauco, Guánica and Guayanilla) and low further away from these urban centers. It would appear that topography is a key factor in predicting forest cover in this system, as has been found elsewhere (Lamb *et al.* 1997, Smith 1997, Trejo and Dirzo 2000). Forest cover was highest in areas with rough topography near to urban centers, while it was low on flat ground further from the urban centers. Flat lands with low forest cover are, for the most

part, active pasture. Unlike the situation that Wickham *et al.* (1999, 2000) analyzed, changes in forest cover do not appear to be driven by land demand – or, rather, that land demand cannot be predicted simply as a function of distance from urban centers. Forest cover reflects land that has been abandoned, and much of what is non-forested is land that was agriculturally productive enough to retain under agriculture. In addition, agriculture is likely to persist on lower-value lands. Higher property values (and as a consequence, property taxes) near urban centers can make agriculture a less viable prospect near cities (although this is likely to be countered by greater ease in getting produce to market).

Landscape Change

Studies of landscape change in the dry tropics are few. Endress and Chinea (2001) looked at land use change in the Republic of Palau in a period of agricultural decline, while (Kramer 1997) looked at changes in what later became the Area de Conservación Guanacaste (ACG), Costa Rica at a time when forest cover was increasing as a direct consequence of programs associated with the formation of the ACG. In contrast, Turner *et al.* (2001) examined land-use change in the southern Yucatan over a time period in which development pressures were high and population was increasing rapidly.

The level of retention of Closed Forest in Puerto Rico was not high compared to most studied landscapes because of the low overall forest cover. Endress and Chinea (2001) and Turner *et al.* (2001) looked at landscapes that were 70-90% forest throughout the study period. Kramer's (1997) work is more comparable in terms of the amount of forest cover, but she subdivided forest types differently making comparisons difficult.

Generally, over the period 1936-1989, agricultural land had a high probability of remaining under agriculture. Transition probabilities to agriculture from other cover classes were low, and remained low throughout the study period.

Transitions 1 2 and 1 3 (Agriculture to Open and Closed Forest respectively) represented the abandonment of agricultural land. In total, the probability of agricultural abandonment remained fairly constant between 1936 and 1983 (ranging from 0.11 to 0.15) but jumped sharply in the final interval (1983-1989) to 0.36. Similarly, transition 1 1 (the retention of agricultural land in agriculture) remained fairly constant in the 1936-1983 period, but declined sharply to 0.62 in the 1983-1989 transition. Throughout this period the probability of retention was much higher in Puerto Rico than it was in the southern Yucatan (where the retention probability was 0.35; Turner *et al.* 2001) and in Guanacaste Conservation Area in Costa Rica (where the retention probability of pasture was 0.41; Kramer 1997). Although the area under agriculture declined sharply (Lugo *et al.* 1996), the retention rate for agricultural land remained high.

The probability of conversion to agriculture from other cover classes (2 1 and 3 1) was low, even when taking into account the relatively small amount of forested land available for conversion. In the Area de Conservación Guanacaste, which saw forest cover increase from less than 15000 ha to over 17000 ha in the period 1979-1985, transition probabilities to pasture remained between 0.09 and 0.25, depending on the forest type (Kramer 1997), while those in the study area in Puerto Rico were in the range 0.01 to 0.13. On predominantly forested landscapes such as those in Palau (Endress and Chinea 2001) and the southern Yucatan (Turner *et al.* 2001) transition probabilities to agriculture were much lower, since the ratio of intact to cleared land is much higher.

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Turner *et al.* (2001) found transition probabilities of only 0.02 from Upland Forest to agriculture, although the transition probability for secondary forest was higher (0.18).

The transition from Closed Forest to Open Forest (3 2) declined over the study period from a high of 0.17 in the first interval (1963-1950/51) to a low of 0.04 in the penultimate interval (1971-1983). This transition is likely to represent biomass harvest – charcoal production, for example – or the degradation of forest by factors such as fire or the incursion of cattle. E.M. Sepulveda (personal communication) reported that his uncle attempted (unsuccessfully) to convert Site 11 to pasture at some time in the past by a combination of cutting and burning of the forested ravine. Actions of this sort could also be responsible for the 3 2 transition. While the use of charcoal as a fuel has declined (Murphy *et al.* 1995), charcoal pits were observed both in fragments (Sites 1 and 2) and on a private farm where *Prosopis pallida* trees in pasture were cut and used to make charcoal. Thus, biomass harvest continues to be a factor in Puerto Rican dry forest fragments albeit at a much lower level than in the past.

With some exceptions (most notably, Coastal Scrub Forest) Open Forest is not a stable natural community in southwestern Puerto Rico. Left to natural processes, most Open Forest is likely to be converted to Closed Forest by succession. In this regard, it is not surprising that Open Forest had consistently lower retention probabilities (between 0.14 and 0.36) than did the other two target land-cover classes (0.62-0.84 for Agriculture and 0.77-0.90 for Closed Forest). In the absence of burning, pasture is likely to become open woodland (Janzen 1988a) through the colonization of spiny trees such as *Prosopis pallida* and unpalatable shrubs such as *Calotropis procera* (Ait.) Ait. f. and *Lantana involucrata* L. These areas are likely to show up as Open Forest in aerial photographs (although pasture dominated by *P. pallida* appeared as Closed Forest in some cases). When these pastures are 'improved' and the trees are cut and burned, the transition from Open Forest to Agriculture is recorded, when in fact the land use has remained pasture throughout the transition.

Dynamics of Focal Fragments

The studied fragments provided a pattern of change that differed from what was observed at the landscape level. Twenty-five of these fragments supported forest cover in 1936. Twenty-three maintained forest cover throughout the period, while two were cleared and subsequently reforested. This suggests that forest fragments have a high 'inertia' – once a patch becomes forested, it tends to remain forested, a fact which agrees with the landscape-level findings. However, 14 of these fragments decreased in size, suggesting that drivers of deforestation remained active even when other land was being allowed to revert to forest. On the other hand, the fact that about half of the deforestation was caused by non-agricultural land transformation suggests that the causes of this deforestation may have been different from the ones that allowed agricultural land to revert to forest. Ramos González (2001) found that built-up areas, forest and shrub land expanded at the expense of agricultural land. Similarly López *et al.* (2001) stated that most urban and suburban development came at the expense of agricultural land.

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Fragment Networks and Connectivity

Figueroa Colon (1996) suggested that Guánica Forest and the Sierra Bermeja were the two main refuges for biodiversity during the period when forest cover was at its lowest extent. When a gap of 1 km between forest patches is considered significant isolation, there is connectivity between these two putative refugia, and it may be assumed that there is gene flow across the landscape. On the other hand, if a 500-m gap is used as the threshold at which connectivity ends, two gaps exist between these areas (Figure 3.2). Differences in species composition between Relict and Regrowth forest means that realized gaps are likely to be consistently larger for many species.

The occurrence of gene flow across the landscape is a stochastic process. The bigger the gap between two forest patches, the lower the probability of gene flow across the gap. In addition, the severity of a gap or even the existence thereof, is a function of the species in question. In the absence of species-specific empirical studies it is difficult to predict thresholds of connectivity across the landscape. The only fragment that is separated from other forest patches by a gap of more than 1 km is Site 9, one of the most species-poor fragments studied (Chapters 4, 7). However, it also differed from other fragments in several important ways (see Chapters 4 and 7). Differences in community structure may be a function of environmental conditions and may not reflect isolation alone. Whatever the thresholds may be, if maintenance of some degree of connection between Guánica Forest and the Sierra Bermeja is seen as a priority, protection of the forest fragments between them is a priority. Two key areas are the strip of hills that run north of the resort town of La Parguera and the strip of forested hills immediately south of Carretera 16 in the Lajas Valley (Figure 3.2, Clusters 4, 5 in Table 3.4). These areas lack form

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lack formal protection for the most part (with the exception of Isla Magueyes which is owned by the Fundación Puertoriqueña de Conservación (Puerto Rico Conservation Foundation) and are likely to be subject to development pressures as the town of La Parguera grows.

Implications

Forest recovery in Puerto Rico has been one of the major exceptions in the global pattern of tropical deforestation, but not the only exception. Important threats to the island's forests remain including urbanization (López *et al.* 2001). In a recent study of land-use change in northeastern Puerto Rico, Ramos González (2001) found that while forest cover increased by 1.2% annually between 1978 and 1995, built-up areas increased by 1.8% per annum. Most of these changes came at the expense of agricultural land and pasture, with the net effect of bringing urban and suburban development into immediate proximity with forest. As a consequence, future expansion in urban and suburban development is likely to come at the expense of forested land.

In the study area, several examples of this are evident. The community of La Luna, which was established by families that were resettled from within Guánica Forest, has grown to the point where it immediately abuts Guánica Forest (Lugo *et al.* 1996). The creation and expansion of Barrio Belgica created Sites 7, 10 and 31; the area occupied by the community was formerly a forested hilltop. Site 35 was eliminated for housing construction, while the land formerly occupied by Site 24 was offered for sale as housing lots after the forest was cleared. The construction of homes also appears to threaten Sites 4 and 14, while Sites 21 and 36 appeared to be earmarked for subdivision

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for housing lots when the fragments were visited in 1997. Between 1936 and 1993 urban and infrastructural development were the factors responsible for most fragmentation and shrinkage of the forest fragments that were the target of this study. Given the demise of agriculture in Puerto Rico, urban development can be expected to be the main threat to the future of forests. The limited area of forest that remains means that the threat to forest remains high. On predominantly forested landscapes, the probability of any given patch of forest being eliminated is fairly low; even if the absolute rate of deforestation is high, the relative rate is likely to be lower than in a largely deforested landscape.

While many studies have attempted to use remotely sensed data alone to infer extinction risks and predict extinction trajectories (*e.g.*, Ranta *et al.* 1998, Tole 2002), the factors that influence the relationship between species richness and area are still not well enough understood to confidently make such predictions. The distribution of species across the landscape is driven by factors such as resource availability, dispersal limitation and extinction debt. Conservation decisions need to reflect the actual patterns of species distributions within communities. The remaining chapters attempt to incorporate these factors.

Summary

1) Forest cover was 23.2% in the dry forest zone in 1993; 18.0% Closed Forest and 5.2% Open Forest.
2) A total of 308 Closed Forest fragments totaling 13100 ha and 312 Open Forest fragments totaling 3800 ha were mapped.

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3) Fifty-two percent of all forest fragments were below 5 ha in area, but only accounted for 4% of the forest area; 3% of all forest fragments were over 100 ha, but accounted for 63% of the total forest cover.

4) Forest cover peaked toward the middle of the dry forest zone and declined toward the eastern and western extremes.

5) Twenty-nine of the forty fragments that formed the basis of the more detailed study maintained some forest cover throughout the period 1936-1993. Nineteen fragments were classified as Relict (> 75% 'old growth'), three were classified as Mixed (25-75% 'old growth') and seventeen were classified as Regrowth (< 25% 'old growth').

6) Twenty-three of the focal fragments increased in size in the period 1936-1993, fourteen decreased in size, and two remained about the same size. Four fragments were eliminated in the period 1995-1998.

7) On the basis of using a 500-m separation as the basis for 'isolation' between fragment clusters, nine distinct clusters were identified on the landscape. On the basis of a 1000-m separation, only two clusters were present;

8) Contrary to expectations, the probability of conversion of forest to non-forest was relatively high in the 'recovering' landscapes of Puerto Rico and Guanacaste, Costa Rica, but was very low in the 'deforesting' landscape of the southern Yucatan; this reflects the limited area of forest on the 'recovering' landscapes rather than a high level of deforestation.

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CHAPTER 4: COMMUNITY STRUCTURE OF PUERTO RICAN DRY FORESTS

Introduction

In the rain shadow created by the mountainous spine of the island (the Cordillera Central), Puerto Rico's south coast is dry. Ewel and Whitmore (1973) classified this area as subtropical dry forest (*sensu* Holdridge 1967). These dry forests originally covered a strip along the south coast about 120 km long (from west to east) and three to 20 kilometers inland (Ewel and Whitmore 1973). Most studies of the plant ecology of this system have focused on Guánica Forest, a 4000-ha protected area (*e.g.*, Ewel 1971, Lugo *et al.* 1978, Dunevitz 1985, Lugo and Murphy 1986, Murphy and Lugo 1986b, 1990, Castilleja 1991, Quigley 1994, Murphy *et al.* 1995, Dunphy 1997, Molina Colón 1998, Dunphy *et al.* 2000). Little has been done to document the extent or ecology of dry forest outside of this protected area (Murphy *et al.* 1995), although Vázquez and Kolterman (1998) have described the vegetation of the Punta Guaniquilla Nature Reserve at the northwestern corner of the dry forest zone.

The most common forest association in Guánica Forest, the Deciduous Forest association, is the best studied. Murphy and Lugo (1986b) found this community to be characterized by a large number of relatively small-stemmed trees, with 56.9% of all stems belonging to multi-stemmed individuals. This was attributed to historical cutting of the trees, but Dunphy *et al.* (2000) found evidence to suggest that this may reflect the natural growth form of many of these species. The other major associations are less well studied. The Semi-Evergreen association has taller trees with fewer stems per individual

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(Lugo *et al.* 1978, Castilleja 1991) while the Scrub Forest association is more open, with more widely spaced trees (Lugo *et al.* 1978, Castilleja 1991).

Forest fragments outside of Guánica Forest are likely to have originally supported forests that were broadly similar to the associations present in Guánica Forest (Gleason and Cook 1926). However, these areas have experienced a wide range of disturbances; much of the dry forest present outside of Guánica Forest is secondary forest *sensu* Corlett (1994) – that is, forests that have developed after agricultural abandonment (see Chapter 3). If the successional trajectories of these forests are similar to what Molina Colón (1998) and Erickson *et al.* (2002) have documented within Guánica Forest (and Roth, 1999 has described in the Dominican Republic), where 50-year-old forests on abandoned agricultural land are species-poor and dominated by exotic leguminous trees, then there is likely to be a large difference between the community compositions of Relict and Regrowth forest fragments (see Chapter 3 for a definition of these terms). On the other hand, if successional trajectories are more similar to what Ray (1993) described in older sites in the U.S. Virgin Islands, where 50-150-year-old successional forests on abandoned agricultural land were dominated by a species-rich mixture of native species, then Relict and Regrowth fragments are likely to be less different, and instead form a continuum in terms of species composition.

Nested Subsets in Fragmented Communities

While species-area curves describe the overall pattern by which species richness scales with increasing areas, they do not describe the overall patterns in species occurrence on a landscape. The theory of island biogeography (MacArthur and Wilson

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1967) predicts how species richness will scale with area in an archipelago, but it does not predict how species will distribute themselves. As Simberloff and Abele (1979, 1982) pointed out, the number of species present in an archipelago is a function of the degree of overlap between the species compositions of individual islands.

Nested subset theory (Patterson and Atmar 1986) predicts that species distributions within archipelagos are likely to be nested. The species present in any given island will be present in all islands that are more species-rich, and all species present in more species-poor islands will be present in that island. The species composition of islands is thus considered to be deterministic.

Extinction, colonization, disturbance, habitat distribution, hierarchical niche relationships and passive sampling can all produce nested patterns (Patterson and Atmar 2000, and references cited therein), but these patterns are especially apparent in extinction-driven systems. The studied fragments are a mixture of relict patches of forest (where species composition is likely to be driven by extinction) and regrowth on abandoned agricultural land (where species-composition is likely to be driven by colonization; see Chapter 3 for a detailed history of the studied fragments). Nestedness as a community characteristic does not seem to have been described for dry forest plant communities, but can it yield information on the incremental conservation value of protecting additional fragments smaller than those that are already protected.

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Objectives

1) To determine whether the fragments support a species-rich native forest community or whether they are simply depauperate stands dominated by weedy exotic species;
2) To determine whether the basal areas and stem densities of the fragments are comparable with those found in Guánica Forest;
3) To determine whether distinct assemblages can be delineated on the basis of their plant species composition;
4) To evaluate the degree of nestedness present in the assemblage of dry forest fragments.

Methods

Data Collection

Vegetation structure, species composition and abundance data were collected from a total of 40 dry forest fragments and in reference plots located in the semi-evergreen, deciduous and scrub forest associations in Guánica Forest. Structure and abundance data were not collected from two of these sites (Sites 31 and 32) and a complete species list was not compiled for Site 3. Methods of site selection and data collection are described in Chapter 2.

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Community Characterization

Dominance-diversity curves (Whittaker 1965) were constructed for the 38 fragments for which abundance data were collected and for the reference plots in Guánica Forest. Relative abundance of each species was calculated within a pooled sample of all plots collected at a single site. In keeping with Hubbell's (2001) definition of a "guild" for plant species (all species competing for a fixed pool of resources, in this case interpreted broadly) comparisons were limited to plants rooted in the ground. Epiphytes and hemi-parasites were thus excluded.

Basal areas were calculated from diameter at breast height (dbh; measured at a height of 1.5 m) measurements of stems ≥ 1 cm, and were expressed as square meters per hectare. Data were pooled across plots and the basal area per fragment was calculated based on the total pooled sample area, rather than on the mean of the plots. The multi-stemmed nature of the community was also investigated.

Jaccard's coefficient of community (Jaccard 1900) was calculated for the 39 fragments for which complete species lists were compiled. Hierarchical clustering with complete linkage was used to group these fragments on the basis of their Jaccard coefficients (see Legendre and Legendre 1998).

Nestedness in Fragment Species Assemblages

The degree of nestedness in this overall assemblage of species was measured using the Nestedness Temperature Calculator (Atmar and Patterson 1995; see Atmar and Patterson, 1993 for the underlying theory). The extent to which the assemblage deviates from p

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from perfect nestedness (the amount of disorder in the system) is termed the "Temperature" of the presence-absence matrix.

The software (Atmar and Patterson 1995) calculated "Temperature", a measure of the unexpectedness in the presence-absence matrix was calculated across species and fragments. The presence-absence matrix was arranged into a state of maximal nestedness by re-ordering entire rows and columns until unexpectedness in the occurrence of species was minimized. The top row thus represented the most "hospitable" fragment and the bottom row the least hospitable one. The left-most column was occupied by the most widespread species, and the right-most column the least widespread one. The "boundary line" is the hypothetical line that separates the portion of the matrix that is expected to be occupied from the portion of the matrix that is expected to be unoccupied.

Local unexpectedness of cell *ij* was calculated according to the formula:

$$u_{ij} = (d_{ij}/D_{ij})^2$$

where d_{ij} measures the distance of the cell from the boundary line along the skew diagonal and D_{ij} is the length of the matrix parallel to the skew-diagonal.

Total unexpectedness was calculated according to the formula:

$$U = 1/(mn)\ \Sigma\ \Sigma\ u_{ij}$$

where m is the number of rows and n the number of columns.

System temperature, T was calculated as

$$T = k\ U$$

where $k = 100/U_{max}$.

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The probability that this degree of nestedness in this species-site matrix could have been produced at random was tested using a Monte Carlo resampling method (Atmar and Patterson 1993).

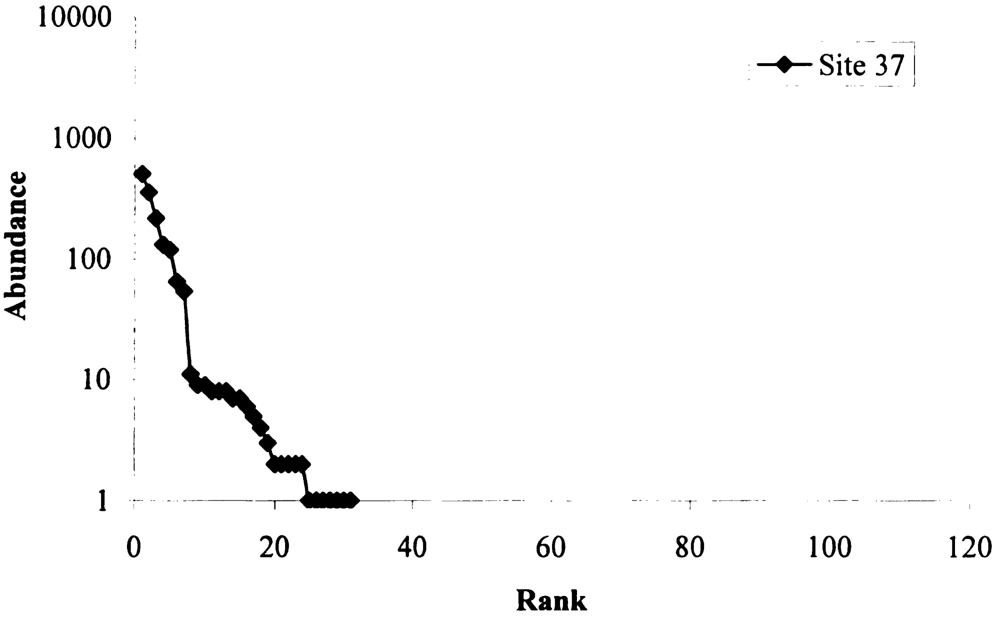
Nestedness Temperature was calculated for plant species in the 39 fragments for which complete species lists were compiled. For comparison purposes, it was also calculated for lizard (Genet 1999b) and termite (Genet 1999a) communities which were studied in a subset of these fragments by other investigators.

Results

Community Characterization

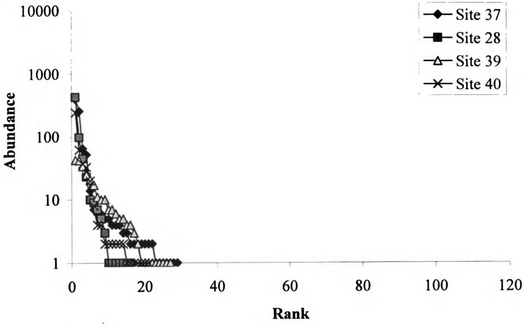
Studied dry forest fragments ranged in size from 6×10^{-3} ha to 1372 ha (see Chapter 3 for details of the history of each of these fragments). Total species richness ranged from 17 to 173 species per fragment. A total of 64511 individuals in 10435 m^2 (380 25-m^2 plots and 4 larger plots ranging from 60-200 m^2 in the fragments and 19 25-m^2 plots in Guánica Forest) were inventoried in species plots. (A further 5142 m^2 were inventoried in transects in which only trees ≥ 1 cm DBH were inventoried).

Dominance-diversity curves showed a large range in terms of their degree of dominance (relative abundance of the most abundant and least abundant species) and their diversity (slope of the curve). Fragments are presented grouped according to hierarchical clustering of Jaccard similarities of species composition (Figure 4.1). The individual curves are presented in Appendix 2.

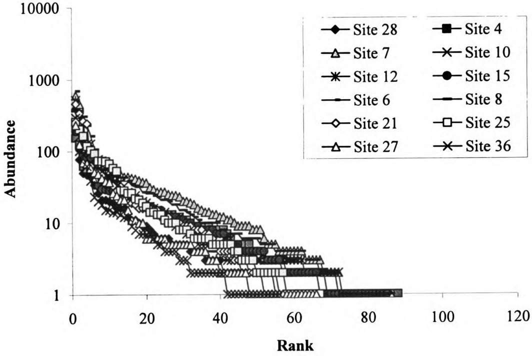


a. Jaccard Cluster 1

Figure 4.1: Dominance-diversity curves for dry forest fragments and Guánica Forest, southwestern Puerto Rico. Fragments are presented grouped according to hierarchical clustering of Jaccard similarities of species composition (see Figure 4.2 and text for details).



b. Jaccard Cluster 2



c. Jaccard Cluster 3

Figure 4.1: (continued).

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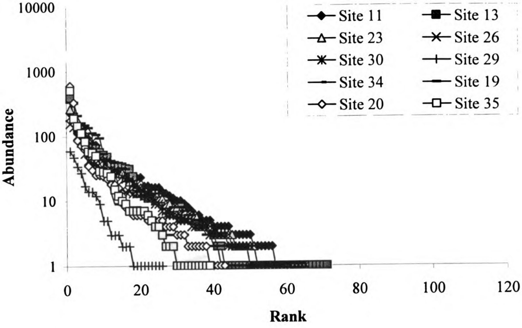
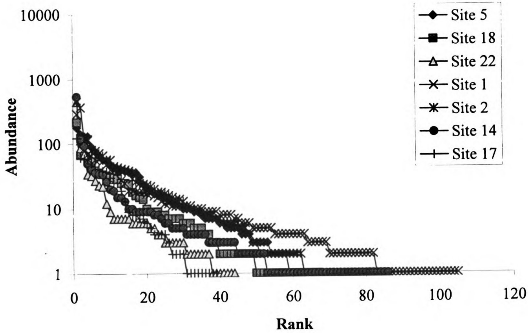


d. Jaccard Cluster 4



e. Jaccard Cluster 5

Figure 4.1: (continued).

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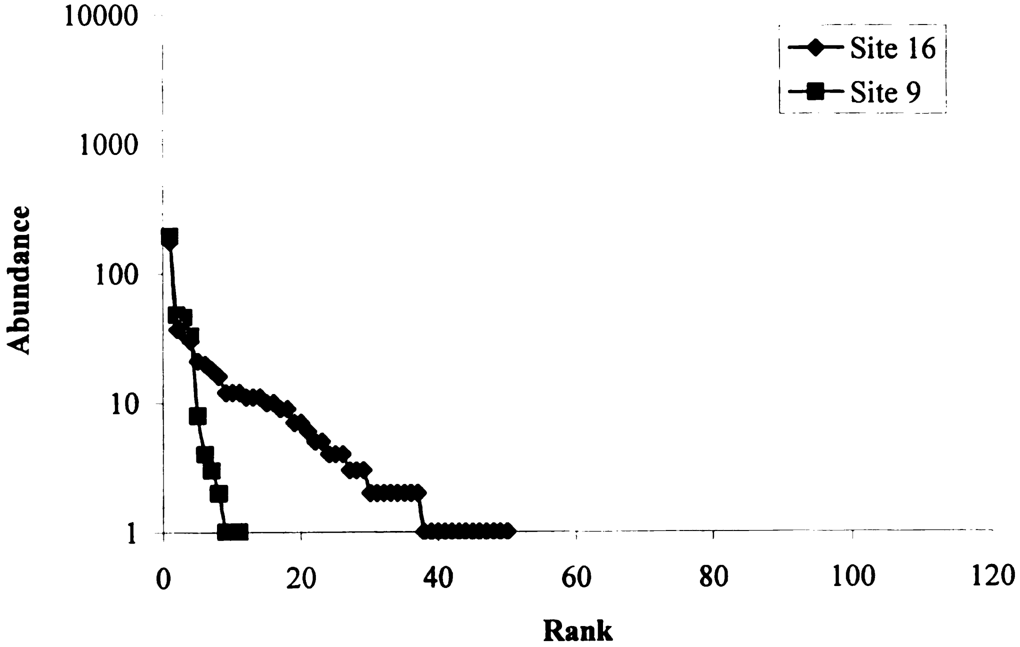
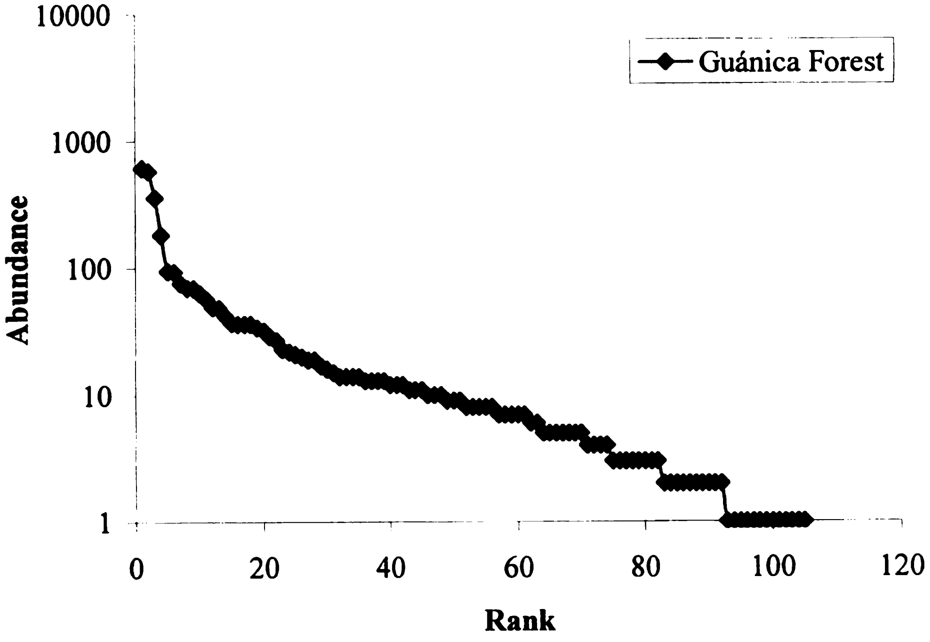


f. Jaccard Cluster 6



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Baseline structural data gathered from the three main forest associations in Guánica Forest are presented in Tables 4.1a and 4.1b. Stems densities ranged from 11275 stems ha^{-1} to 24857 stems ha^{-1} (Table 4.1a) with the Deciduous Forest association supporting the highest stem density. Total basal area (BA) ranged from 16.9 m^{2} ha^{-1} to 25.8 m^{2} ha^{-1} and was highest in the Scrub Forest association. This anomaly appears to reflect the cactus *Pilosocereus royenii*; eight individuals of *P. royenii* accounted for 50% of the basal area of one of the two Scrub Forest transects (40% of the total basal area of the two transects combined). The Semi-Evergreen Forest association had a higher BA than did the Deciduous Forest association. Basal area of the fragments ranged from 5.1 m^{2} ha^{-1} to 47.6 m^{2} ha^{-1} (Table 4.2).

Twelve of the 41 fragments had basal areas that were lower than that of the Deciduous Forest measured in Guánica Forest (stems $\geq$ 1 cm dbh). Nine of these fragments had basal areas lower than the Guánica Forest values when only stems $\geq$ 2.5 cm dbh were considered, although 18 of them had basal areas lower than those recorded by Murphy and Lugo (1986b). When only stems $\geq$ 5 cm dbh were considered, six of the fragments had basal areas lower than the value recorded for Deciduous Forest in Guánica Forest, but 12 of them had basal areas lower than that reported by Murphy and Lugo (1986b).

A total of 11412 stems $\geq$ 1 cm dbh on 4699 trees were measured. Of these, 8797 stems (77.1%) were part of multi-stemmed clumps with between two and 34 stems per tree (Table 4.3). The mean number of stems per tree was 2.43 for all trees and 4.22 for multi-stemmed trees (Table 4.3). Among stems $\geq$ 2.5 cm dbh, 68.3% belonged to

***Table 4.1:** Summary of the structural characteristics of the plant community in Guánica Forest, Puerto Rico based on this study and published data.*

Table 4.1: Summary of the structural characteristics of the plant community in Guánica Forest, Puerto Rico based on this study and published data.

a. Stem density (stems ha^{-1})

	Semi-evergreen Forest			Deciduous Forest			Scrub Forest		
	≥ 1 cm dbh	≥ 2.5 cm dbh	≥ 5 cm dbh	≥ 1 cm dbh	≥ 2.5 cm dbh	≥ 5 cm dbh	≥ 1 cm dbh	≥ 2.5 cm dbh	≥ 5 cm dbh
This Study	11275	5125	1800	24857	9857	1905	18133	8733	4467
Lugo *et al.* (1978)	--	--	2160[a]	--	--	2260 1170	--	--	540
Murphy & Lugo (1986a)	--	--	--	--	12173	2307	--	--	--
Castilleja (1991)	--	3146	--	--	7867	--	--	1556	--
Erickson *et al.* (2002)	--	--	--	13060[b] 11114[b] 3651[c] 7403[c]	--	--	--	--	--

a. Transition between semi-evergreen and deciduous forests associations
b. Mature forest areas that supported closed forest in the 1936 aerial photographs.
c. Secondary forest plots that were agricultural land in the 1936 aerial photographs

b. *Basal Area* (m^2 ha^{-1})

Table 4.1: (continued).

b. Basal Area (m^2 ha^{-1})

	Semi-evergreen Forest			Deciduous Forest			Scrub Forest		
	≥ 1 cm dbh	≥ 2.5 cm dbh	≥ 5 cm dbh	≥ 1 cm dbh	≥ 2.5 cm dbh	≥ 5 cm dbh	≥ 1 cm dbh	≥ 2.5 cm dbh	≥ 5 cm dbh
This Study	20.5	19.2	16.1	16.9	13.6	6.5	25.8	23.9	19.2
Lugo *et al.* (1978)	--	--	10.7[a]	--	--	9.1 6.7	--	--	4.2
Murphy & Lugo (1986a)	--	--	--	(21.2)[b]	17.8	9.4	--	--	--
Castilleja (1991)	--	27.9	--	--	16.0	--	--	3.3	--
Erickson *et al.* (2002)	--	--	--	10.5[c] 14.8[c] 16.8[d] 10.9[d]	--	--	--	--	--

a. Transition between semi-evergreen and deciduous forests associations
b. Total basal area of all stems (not just those above 1 cm dbh)
c. Mature forest areas that supported closed forest in the 1936 aerial photographs.
d. Secondary forest plots that were agricultural land in the 1936 aerial photographs

Table 4.2: Summary of the structural characteristics of studied dry forest fragments: basal area and stem density.

Table 4.2: Summary of the structural characteristics of studied dry forest fragments: basal area and stem density.

	Stem Density (Stems per hectare)			Basal Area (m^2 per hectare)		
	≥ 1 cm dbh	≥ 2.5 cm dbh	≥ 5 cm dbh	≥ 1 cm dbh	≥ 2.5 cm dbh	≥ 5 cm dbh
1	24500	8675	1550	17.6	14.4	7.5
2	18800	7600	2080	17.3	14.7	9.5
3	18440	10880	5000	28.8	27.1	21.5
4	8890	4284	1006	12.2	11.2	7.9
5	18100	5933	2367	25.6	23.3	20.0
6	4567	2800	1200	17.9	17.5	16.0
7	25440	8600	2760	26.2	22.7	17.5
8	8367	4633	2900	24.8	23.9	22.4
9	35760	5040	160	9.5	4.3	0.3
10	8133	4000	1733	17.0	16.2	14.0
11	14900	6750	1250	22.2	20.3	15.6
12	11752	5085	1239	13.1	11.7	8.0
13	11371	5029	1029	9.5		
14	12800	6100	1700	18.5	17.1	12.7
15	10889	5600	1244	20.9	19.8	15.7
16	10333	2900	967	7.8	6.4	4.9
17	16867	2467	267	5.1	2.6	0.8
18	24457	9371	1600	17.7	14.4	7.2
19	6400	4700	2250	23.7	23.3	20.6
20	5300	3750	1900	14.8	14.4	12.5
21	6067	3933	1133	10.9	10.4	7.9
22	29657	6457	1257	22.8	18.5	13.9

Table 4.2: (continued).

	Stem Density (Stems per hectare)			Basal Area (m^2 per hectare)		
	≥ 1 cm dbh	≥ 2.5 cm dbh	≥ 5 cm dbh	≥ 1 cm dbh	≥ 2.5 cm dbh	≥ 5 cm dbh
23	15100	8100	3200	47.6	46.1	41.3
24	6800	3600	700	10.0	9.3	6.3
25	14571	7571	4000	29.7	28.1	24.2
26	7563	4748	2689	13.9	13.3	11.0
27	17067	10467	6333	33.3	31.8	27.9
28	15840	8240	2880	16.5	14.7	9.4
29	9467	6133	3600	23.3	22.6	19.9
30	5134	2723	804	15.7		
33	4900	2100	1100	5.6	5.0	4.3
34	2257	1286	771	18.1	17.9	17.4
35	12202	7890	4495	28.7	27.7	24.1
36	7717	3696	1087	19.4		
37	2750	1800	1500	21.1	20.9	20.7
38	23700	10800	3200	30.7	27.9	20.6
39	10900	5300	3200	22.2	20.9	18.9
40	7000	5000	2833	22.7	22.4	20.3
41	24320	8320	1840	17.5	14.0	8.2

multi-stemmed trees while 45.9% of stems $\geq$ 5 cm dbh were part of multi-stemmed trees (Table 4.3).

The clustering algorithm produced a total of 7 clusters based on a 0.8 cut-off (Figure 4.2). Clusters 1 and 7 each consisted of a single Regrowth fragment (see Chapter 3 for details of the successional history) with unusual species compositions. Cluster 2 consisted of four Regrowth fragments. Cluster 3 consisted of 10 Relict, two Mixed, and one unclassified fragment. Cluster 4 consisted of eight Regrowth and three Relict fragments. Cluster 5 consisted of five Relict, one Mixed and one Regrowth fragment. Cluster 6 consisted of two Relict fragments.

Nestedness in Fragment Species Assemblages

All three species-occurrence matrices were significantly nested. The plant species x fragment matrix consisted of 393 species present in a system of 39 forest fragments with a matrix fill of 19.4%. The lizard x fragment matrix consisted of 10 species in 10 fragments (Genet 1999b) with a fill of 59.5% and the termite x fragment matrix consisted of 9 species in 10 fragments (Genet 1999a) with a fill of 53.8%. The Nestedness Temperature of the species x island matrix was 14.6°, while those of the lizard and termite matrices were 4.16° and 11.31° respectively. Based on Monte Carlo estimation, the probability of a matrix of the temperature of the plant matrix or less being drawn at random was < 0.00001. The probability of a matrix of the calculated temperature or less being drawn at random was less than 2.75×10^{-5} for the lizard matrix and less than 2.15×10^{-5} for the termite matrix.

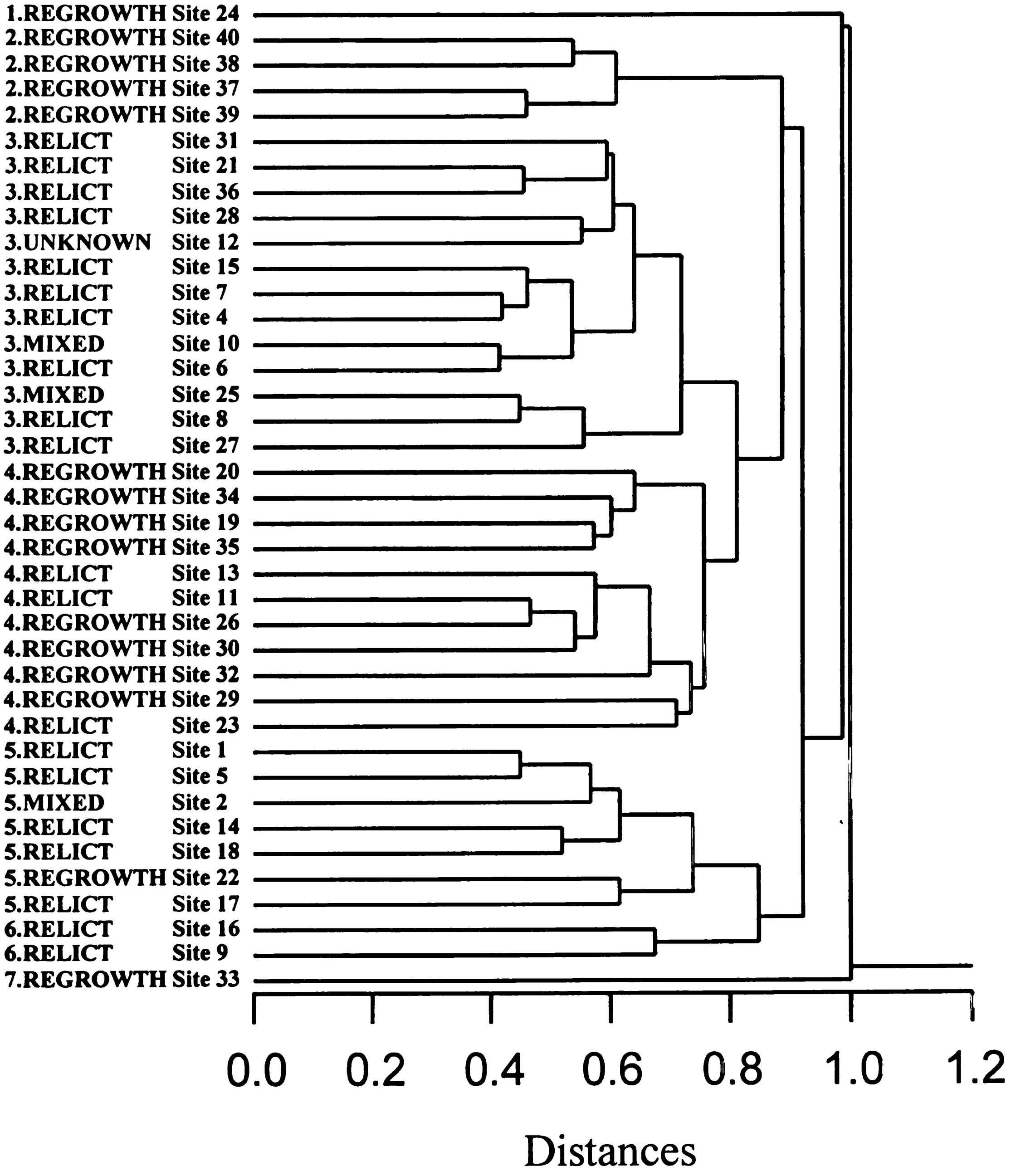

Figure 4.2: Hierarchical cluster dendrograms of Jaccard coefficients based on the species composition of Puerto Rican dry forest fragments, southwestern Puerto Rico. Clusters were delineated on the basis of a cut-off distance of 0.8. Numbers refer to clusters referred to in the text.

Table 4.3: The distribution of stems among single- and multi-stemmed trees in Puerto Rican dry forest.

	Percentage of Trees		Number of Stems per Tree		Maximum Number of Stems per Tree	Percentage of stems in multi-stemmed clumps
	Single Stemmed	Multi-stemmed	Single Stemmed	Multi-Stemmed		
Stems ≥ 1 cm dbh	55.7	44.3	2.43	4.22	34	77.1
Stems ≥ 2.5 cm dbh	63.3	36.7	2.00	3.72	26	68.3
Stems ≥ 5 cm dbh	67.4	32.6	1.95	3.93	23	45.9

Due to the differences between the plant matrix and the animal matrix (in terms of the number and range of fragments sampled) the two results should not be taken to be based on identical samples. However, since all but one of the lizard and termite samples are a subset of the plant plots, some comparisons are certainly warranted.

Discussion

Community Characterization

As is typical of Caribbean dry forests (Murphy and Lugo 1995) both the fragments and the reference plots in Guánica Forest consisted of large numbers of small-stemmed trees (Tables 4.2 and 4.3). As Lugo *et al.* (1978) pointed out, if a cut-off of 10 cm stem diameter (standard in forestry work) were used to characterize this community, there would be very few trees. While a 2.5 cm diameter at breast height (dbh) cut-off has been fairly standard in community studies (*e.g.*, Gentry 1982, Murphy and Lugo 1986b, Gillespie *et al.* 2000), a considerable proportion of the biomass is accounted for by stems between 1 cm and 2.5 cm. Between 0.2 m^2 ha^{-1} and 5.2 m^2 ha^{-1} (or up to 55% of the basal area in stems over 1 cm dbh) is accounted for by stems in this range. This is similar to what Murphy and Lugo (1986b) found in their study in the Deciduous Forest association in Guánica Forest, where stems under 2.5 cm dbh (all measurable stems; they did not use a 1 cm cut-off) accounted for 16% of the total basal area.

The findings of this study for the most part do not deviate from previous studies of Guánica Forest (Lugo *et al.* 1978, Murphy and Lugo 1986b, Castilleja 1991) except in the case of Scrub Forest. Stem densities and basal area in the Scrub Forest differed

sharply in magnitude and pattern from the findings of previous studies. Lugo *et al.* (1978) found the density of stems ≥ 5 cm dbh to be 540 stems per hectare, and the basal area 4.2 m^2 ha^{-1} in the Scrub Forest association. Similarly, Castilleja (1991) found the density of stems ≥ 2.5 cm dbh to be 1556 stems per hectare, and the basal area to be 3.3 m^2 ha^{-1}. Both studies found that the Scrub Forest had the lowest stem density and basal area among the three associations. This is in sharp contrast with the findings of this study in which the Scrub forest had the highest density of large stems and the highest basal area among the three associations.

There are several factors that may be responsible for this lack of agreement. One is the definition of Scrub Forest. There is no study of which I am aware that seeks to define the various associations that are present in Guánica Forest. The associations appear to be a modification of Beard's system of vegetation classification (Beard 1944, 1955) and are fairly intuitive, but they represent real communities that blend into one-another, usually without sharp borders. As a consequence of this, it is possible that I defined Scrub Forest more broadly than did other authors, with the result that my sample included more large trees than did the previous studies. While this explanation may account for some of the differences in basal area between this study and previous studies, it fails to account for the qualitative differences. I found that Scrub Forest had the largest basal area of all the associations. Thus, the discrepancy cannot simply be explained in terms of the use of a broader definition of Scrub Forest than other studies. Another possible explanation for this discrepancy lies with the fact that sample areas are relatively small. While both Lugo *et al.* (1978) and Castilleja (1991) used a sample area of 1000 m^2, this study used a 300 m^2 sample; however, the fact that a smaller minimum stem diameter was used in this study means that similar numbers of stems were measured in all three studies.

Whether the sample measured was large enough to obtain a stable estimate of stem density or not, the major factor influencing stem density and basal area estimates for the Scrub Forest association was the cactus *Pilosocereus royenii.* If the eight individuals of this species had not been present in the sample the estimated basal area would have been 15.5 m^2 ha^{-1}. This would have resulted in a pattern that qualitatively agreed with previous studies, with Scrub Forest having a lower estimated basal area than the Deciduous Forest or Semi-Evergreen Forest associations. On the other hand, there is no reason why these individuals should be excluded – this species is, in fact, one of the characteristic species of the Scrub Forest association (Lugo *et al.* 1978, Castilleja 1991).

Five fragments had extremely low basal areas (< 10 m^2 ha^{-1} based on stems ≥ 1 cm dbh; Table 4.3). Three of these (Sites 9, 16 and 17) were coastal fragments with fairly open canopies resembling Scrub Forest. The other two were disturbed fragments.

Fragments differed substantially in terms of species-abundance relationships. As illustrated in Figure 4.3, the difference between the most diverse (Sites 4 and 5) and the least diverse (Sites 9 and 38) fragments are substantial, both in terms of the relative abundance of the dominant species and in terms of the overall diversity of the sampled species. The fact that sample sizes were unequal between species-rich and species-poor fragments confounds the relationship (a larger sample increases the probability of encountering rare species) but it is still apparent that there are marked differences in species diversity among fragments (see Appendix 2).

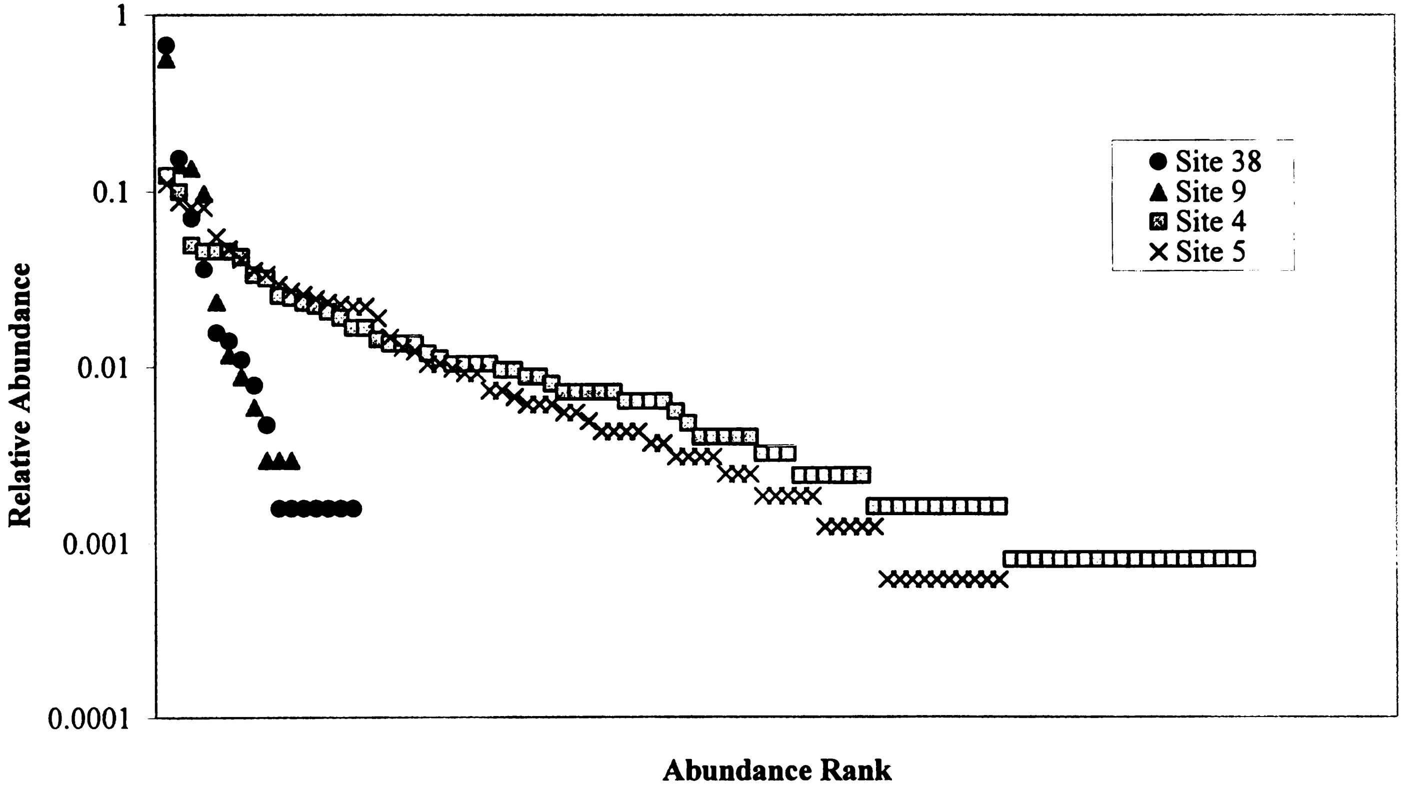

Figure 4.3: Dominance-diversity curves for four dry forest fragments in southwestern Puerto Rico. Site 38 (circles) and Site 9 (triangles) are the two lowest-diversity fragments, while Sites 4 (squares) and 5 (crosses) are among the highest diversity.

The clustering algorithm produced three large clusters and four small clusters when the cut-off distance of 0.8 was used (Figure 4.2). In reality, two fragments (Site 24 and Site 33) were not assigned membership in any cluster and were only joined to the other clusters at a distance of 1.0 (which amounts to a similarity of 0.0). Thus Clusters 1 and 7 are simply fragments that were not assigned to any cluster. They were also not similar to one-another. The deepest cleavage among the other clusters is between Clusters 2, 3, and 4 on one hand, and Clusters 5 and 6 on the other. Cluster 2 was a group of small Regrowth fragments each centered on a single *Pisonia albida* tree. Cluster 4 included the remaining Regrowth fragments and two disturbed Relict fragments. These fragments were dominated (to varying extents) by *Leucaena leucocephala*.

General observations of secondary dry forest in southwestern Puerto Rico suggest that there are two or three successional pathways possible on abandoned agricultural land. The most common type involves *Leucaena leucocephala* and *Prosopis pallida*. *P. pallida* is a common pasture tree; cattle will eat it and disperse its seeds (Janzen 1986a). Active pasture can develop a continuous canopy of *P. pallida* (personal observation). Abandoned pastures are invaded by *L. leucocephala*, resulting in a simplified community that appears to be stable, at least in 50-year-old abandoned agricultural land (Molina Colón 1998). In a similar situation in St John, U.S. Virgin Islands, Ray (1993) found that a 33-year-old abandoned pasture was dominated by *L. leucocephala* while a 50-year-old pasture had a more species-rich community dominated by *Bourreria succulenta*. Ray (1993) hypothesized that the difference was a consequence of grazing by feral donkeys in the *L. leucocephala* site which was arresting succession. However, Molina Colón (1998) found a species-poor community dominated by *L. leucocephala* on 50-year-old agricultural land in the absence of grazing. This suggests that this community is fairly stable and not just a transient successional assemblage.

An alternative successional pathway, which appears to involve *Pisonia albida*, is typified by Cluster 2. Patches of *P. albida*-dominated regrowth are often nested within larger areas of *L. leucocephala*-dominated regrowth and can also develop in active pasture (personal observation). These patches show a marked difference in species composition relative to the surrounding *L. leucocephala*-dominated regrowth; they are much more species rich and often consist of fleshy-fruited trees. While both *Leucaena leucocephala* and *Pisonia albida* are dry fruited, *P. albida* often shows high levels of infestation with mistletoes (*Phoradendron* spp.) These fleshy-fruited hemi-parasites will attract frugivores (Watson 2001) and thus enrich the seed rain under *P. albida* trees (Guevara *et al.* 1986, Guevara *et al.* 1992, Guevara and Laborde 1993). See Janzen (1988a) for a description of the process by which 'nuclear trees' can develop into forest islands.

A third successional pathway may involve colonization by *Bourreria succulenta.* Ray (1993) found a 50-year-old pasture to be dominated by *B. succulenta.* Similarly, in Puerto Rico, disturbed areas can be dominated by this species. No fragments were distinctly dominated by this species, but roadside areas and bulldozed areas adjacent to one fragment (Site 14) were dominated by this species. As a fleshy-fruited species, *B. succulenta* should be attractive to frugivores, which are likely to deposit a seed-rain rich in fleshy-fruited species.

The proportion of trees that were multi-stemmed (44.3%) was consistent with previous studies; Dunphy *et al.* (2000) found 43.3% of all trees were multi-stemmed. Similarly, Murphy and Lugo (1986b) found that 57% of all stems ≥ 2.5 cm dbh were members of multi-stemmed individuals. This is smaller than the values of 68.3% for stems ≥ 2.5 cm dbh and 77.1% for stems ≥ 1 cm dbh that I found in this study.

The average number of stems per individual ranged from 1.95-2.43 depending on whether a 1 cm, 2.5 cm or 5 cm minimum diameter was employed. Similarly, the number of stems per multi-stemmed tree ranged from 3.72-4.22.

The method used here is an underestimate of the number of trees that are multi-stemmed since it is based on a cut-off diameter at breast height of 1 cm. Several trees that are reported as being single stemmed had additional stems that were below the 1 cm cut-off (personal observation). In addition, the proportion of single-stemmed trees is higher than might have been found if the sample were restricted to Relict fragments since *Leucaena leucocephala*, which dominated most Regrowth fragments, is generally single stemmed.

Nestedness in Fragment Assemblages

As expected, the system shows significant nestedness, not just for plant species, but also for animal species. The very low Nestedness Temperature (high degree of nestedness) indicates that fragments with fewer species have a subset of the species that are present in more species-rich fragments. This means that smaller fragments are unlikely to add species that are absent from larger fragments. While secondary growth on abandoned agricultural land has fewer species than older forests, these species are also present in relict vegetation. Many of these species are components of the native forest (or at least they appear to be in modern disturbed forests). Others, like *Leucaena leucocephala*, are exotic species, but have either successfully invaded disturbed relict forest, or have colonized the edges of expanding fragments. When the comparisons are made between inventory lists, these species appear as part of the vegetation of all fragments.

These issues are expanded and further discussed in Chapters 5 – 7.

Summary

1) Relict fragments supported a species-rich assemblage that was dominated by native plant species; Regrowth fragments supported fewer species and many were dominated by exotic species, especially *Leucaena leucocephala*.
2) Like other dry forests, both the fragments and Guánica Forest consisted of high densities of small, multi-stemmed trees; much of the basal area was accounted for by small trees. Although overall stem densities and basal areas of Guánica Forest and the fragments fell within the range observed in previous studies, the estimated basal area for Scrub Forest in Guánica Forest was not consistent with either expectations or previous studies.
3) Five distinct clusters (and two unassigned sites) were found among the fragments on the basis of a matrix of Jaccard similarities. These included three predominantly Relict community types (including one coastal community) and two predominantly Regrowth community types (one dominated by *Leucaena leucocephala* and one dominated by *Pisonia albida*). Overall there appeared to be a real separation between

Relict and Regrowth fragments on the basis of species composition, although the main Regrowth cluster was nested between two clusters of Relict fragments; Mixed fragments were not distinct from Relict fragments on the basis of species composition.

4) Nested subset analysis found that fragment communities were significantly nested (as were lizard and termite communities in a subset of the fragment assemblage).
5) A large proportion (44.3%) of all trees was multi-stemmed. Trees averaged 2.43 stems per tree; multi-stemmed trees averaged 4.22 stems per tree. The tree with the largest number of stems, 34, was a *Coccoloba microstachya* individual present in Site 21.

CHAPTER 5: SPECIES-AREA RELATIONSHIPS OF PUERTO RICAN DRY FOREST PLANTS ON A FRAGMENTED LANDSCAPE.

Introduction

The increase in species-richness with increasing area is considered one of the closest things to a general rule in ecology (Schoener 1974, Lomolino 2000). This relationship is most commonly formalized using the power function or Arrhenius equation (Arrhenius 1921) $S = cA^z$ (where S = number of species in an area of size A, and c and z are fitted constants). Values of the parameter z usually range from 0.1 to 0.5 (Rosenzweig 1995). Values at the lower end of the range are common in samples taken from continuous habitat while those taken from islands within an archipelago are usually around 0.26 (the 'canonical' value found by Preston, 1962). Values are higher when environmental thresholds are crossed, and are highest when they include areas that draw on different source pools (*i.e.*, when evolution plays a different role in structuring the biotas of different areas).

While there is an established body of theory regarding the value of the parameter z, there is none regarding the parameter c (Lomolino 2000). Mathematically, $S = c$ when $A = 1$. Thus, it appears reasonable to consider c to be a measure of species per unit area (or, as such, 'species density'); Hubbell (2001) equated c with ρ, the number of species per unit area. Since species per unit area is a function of the units of area used, it is reasonable that values of c should vary over orders of magnitude, as Lomolino (2000) pointed out, depending, for example, on whether the unit of measurement is square meters or square kilometers. While the power function is the most common model of the species-area relationship, others are also used. The semi-log or Gleasonian model (Gleason 1922) $S = k0 + k1 \log A$ (where $k0$ and $k1$ are fitted constants) is often used in plant ecology (Rosenzweig 1995, Lomolino 2000). Less theory exists regarding these constants than about those of the Arrhenius equation. Both of these models have been criticized on two grounds: that they are unbounded (the relationship does not asymptote), and that they do not account for the 'small island effect'.

Several criticisms of the power function as a model of the relationship between species richness and area derive from the idea that species-area curves should asymptote. The assumption is that island biotas are drawn from finite species pools, and as such should not increase indefinitely. An equation that adequately models the species-area relationship should, thus, asymptote. One weakness in this criticism that has been pointed out by He and Legendre (1996) is that it is statistically unwarranted to use a regression curve to extrapolate beyond the range of the data. It should not matter what a species-area curve predicts beyond the range of the data. While some of the criticisms that the power function vastly overestimates the species richness at large scales are based on fitted data (Plotkin *et al.*2000), in other cases they are based on extrapolated predictions from much smaller samples. Thus, the criticism may be based on a failure of the model to perform when used improperly – more a criticism of the methodology than of the model. In addition, as Hubbell (2001) pointed out, there is room for an infinite number of species among infinite individuals in infinite area. Thus, despite what has been said elsewhere, the idea that species-area curves should tend towards infinity rather than asymptote should not be problematic in and of itself. However, most people think in terms of the fact that a finite area will have a finite number of species, and expect that all of those species will be found before the final plot is sampled. From this idea comes the expectation that any real species-area curve should asymptote.

The expectation that species-area curves should asymptote may also reflect a bias that comes from working in species-poor systems (usually in the Temperate Zone). Species-area curves do not asymptote in even the largest data sets for moist tropical forest trees (Condit *et al.* 1996, He *et al.* 1996, Plotkin *et al.* 2000). While it has been argued that the power function overestimates species-richness at large scales (May 1975, He and Legendre 1996, Plotkin *et al.* 2000), it has also been observed that species-area curves tend upward at larger spatial scales, when areas with different evolutionary histories are included (Preston 1962, Shmida and Wilson 1985, Rosenzweig 1995, Hubbell 2001).

The existence of a small island effect (SIE) is a valid concern with regards to the use of the power function to model the species-area curve. Unfortunately, there seems to be disagreement as to what form an SIE should take. According to Lomolino and colleagues (Lomolino 2000, Lomolino and Weiser 2001), the SIE is the lack of a relationship between species richness and area in small islands; many small islands have fewer species than are predicted by the power function. However others (May 1975, He and Legendre 1996, Plotkin *et al.* 2000) have found that there was a lack of fit of the power function in small islands because the observed slope of the species-area curve was steeper than the predicted curve.

MacArthur and Wilson (1967) noted that species richness is independent of area for relatively small islands. Williams (1996) pointed out that many small islands have no species, and their omission from species-area curves biases our view of species-area relationships. As a consequence of this, Lomolino (2000) makes a case for the use of sigmoidal models of the species-area curve, and in particular recommends the sigmoidal $\text{Hill}_{\text{Slope}}$ function as a model with biologically meaningful parameters. He and Legendre (1996) had a different idea of the small island effect; they expected small fragments to have steeper species-area curves because they are prone to lose species more rapidly than are larger fragments. These two views may be reconciled of one considers the former to be the case in a system which is stable or accreting species, while the latter is the case in a system which is losing species after fragmentation.

The applicability of the idea of the small island effect to plant species in forest fragments is questionable. When studies of fragmentation look at species on islands or animals in forest fragments, it is possible to have zero species richness in non-zero area. An island might support no species (or no species in the target taxon) and a forest fragment might lack the group of animals upon which a study focused. However, if a study focuses on the plant species composition of a forest fragment (as this one did) it is impossible to have zero species richness in non-zero area. Once there is something which can be called a forest fragment, at least one tree species must be present. In fact, plant species are likely to be present even in the absence of trees – thus, fragments could be considered to have non-zero species richness when the fragment size is equal to zero.

One aspect of the construction of species-area curves that is rarely addressed is the fact that there are really two types of species-area curves (but see Hubbell 2001). Studies that look at an archipelago of islands (or fragments) tend to construct species-area curves with each island as a separate point in the regression. Each island is an independent sample, and only the species richness (not the species composition) is considered. On the other hand, when species-area curves are constructed within a single patch (*e.g.*, collectors curves) points are often nested or averaged. He *et al.* (1996) and Plotkin *et al.* (2000) constructed species-area curves based on subsets of a larger 50-ha plot. In some cases average species richness per plot is calculated for each size-class, while in other cases plots are random-ordered and species-area curves are calculated through Monte Carlo re-sampling. In yet other cases, simple collectors' curves are employed: the species-area curve is constructed on the basis of the order in which plots are collected. These two types of species-area curves may be termed cumulative or nested species-area curves (in the latter case) and non-nested curves (in the former case). There are fundamental differences (both biological and statistical) between these two types of species-area curves, yet I have never seen this difference acknowledged, let alone seen it actually investigated. The degree to which a system is nested (see Chapter 4) will determine the degree of divergence between these two types of species-area curves.

Objectives

1) To explore the relationship between plant species richness and area in studied dry forest fragments;
2) To compare the effectiveness of a power function (Arrhenius equation) and a sigmoid function (the $\text{Hill}_{\text{Slope}}$ function) as suggested by Lomolino (2000) as models of the species-area curve;
3) To investigate the relationship between the per-plot species richness ("species density" *sensu* Whittaker, 1975) and total species richness in studied dry forest fragments.

Methods

Data Collection

Data on vegetation structure, species composition and species abundance were collected from a total of 40 dry forest fragments. Species compositions were recorded for a total of 380 25-m^2 plots in 35 of the fragments and 19 25-m^2 plots in three reference communities in Guánica Forest. The selection of study sites and the methods of data collection are described in Chapter 2.

Data Analysis

Inter-fragment species-area curves were modeled by means of a power function of the form

$$S = cA^z$$

(Preston 1962, MacArthur and Wilson 1967) where S represents the species richness of the fragment, A represents the area of the fragment in hectares and c and z are fitted parameters. The parameters were estimated by maximum likelihood nonlinear regression of the untransformed data.

To examine the effects of unequal levels of error (based on the fact that species lists would be more complete in smaller sites, as a consequence of the sampling method) and to look for discontinuities in the underlying species-area relationship, regressions were calculated for subsets of the fragment array: < 100 ha, < 10 ha, < 5 ha, < 1 ha, < 0.5 ha and for the fragments and Guánica Forest combined. Separate analyses were also carried out on the basis of fragment history (see Chapter 3 for a description of the land-use history of each of the fragments over the period 1936-1993).

Additional species-area curves were fitted using the $\mathrm{Hill}_{\mathrm{Slope}}$ function (Lomolino 2000):

$$S = S_{\max} / [1 + (\mathrm{Hill}_{\mathrm{Slope}}{}^{(\mathrm{Log}\,(A50\,/\,\mathrm{Area}))})]$$

where $S_{\max}$ is the maximum species richness or asymptote, $\mathrm{Hill}_{\mathrm{Slope}}$ is a direct measure of the slope of the curve through the inflexion point, A50 is the area yielding a species richness that is half the maximum value and Area is the fragment area.

The curves were fit with $S_{\max}$ unfixed and with $S_{\max} = 393$ (the actual number of species recorded in the array of fragments) and $S_{\max} = 650$ (the total number of species recorded for Guánica Forest according to Figueroa Colon (1996). Curves were fit for the fragments alone and for the fragments and Guánica Forest combined.

The relationship between the number of species per 25-m^2 plot ('species density' *sensu* Whittaker, 1975) for the 35 fragments for which inventories based on 25-m^2 plots were carried out (see Chapter 2 for details of the data collected in each fragment) and fragment species richness, fragment area and fragment history (see Chapter 3 for details of the history of these forest fragments) was investigated using analysis of variance (ANOVA).

Intra-fragment species-area curves (species accumulation curves) were constructed for each of the 35 fragments for which inventories based on 25-m^2 plots were carried out (see Chapter 3 for details of the data collected in each fragment) and for the three reference communities in Guánica Forest. Species-area curves were created using a re-sampling method: in each fragment, the curves were constructed by random-ordering the samples. Five sets of random-ordered plots were combined to make a single species-area curve. Curves of the form $S = cA^z$ were fitted using non-linear regression. All analyses were carried out using Systat 9 (SPSS Inc., 1998).

Results

Initial examination of the data suggested that there might be confounding in the data set between fragment size and history, since most of the Regrowth fragments are small and most of the large fragments are Relict. However, examination of a General Linear Model analysis of the relationship between Species Richness, Fragment Area and Fragment History revealed that there was no significant interaction between Area and History in the linearized (log-transformed) data (Table 5.1a). When the complete model was analyzed, History was not significant ($p<0.085$), but when the (nonsignificant) interaction term was omitted, Fragment History was a significant predictor of Log Fragment Species Richness (Table 5.1b).

Table 5.1: Results for a General Linear Model analysis of the relationship between fragment species richness, fragment area and fragment history (see text for definitions of the terms).

a. Analysis of the complete model

Source	Sums-of-Squares	df	Mean-Square	F-ratio	P
Fragment History	1.352	1	1.352	17.389	0.085
Log Fragment Area	0.414	2	0.207	2.662	< 0.001
Status*Log Fragment Area	0.281	2	0.141	1.809	0.180
Error	2.847	32	0.078		

Table 5.1: (continued)
b. Analysis of the model without the non-significant interaction term

Source	Sums-of-Squares	df	Mean-Square	F-ratio	P
Fragment History	0.722	2	0.361	4.437	0.019
Log Fragment Area	2.580	1	2.580	31.680	< 0.001
Error	2.768	34	0.081		

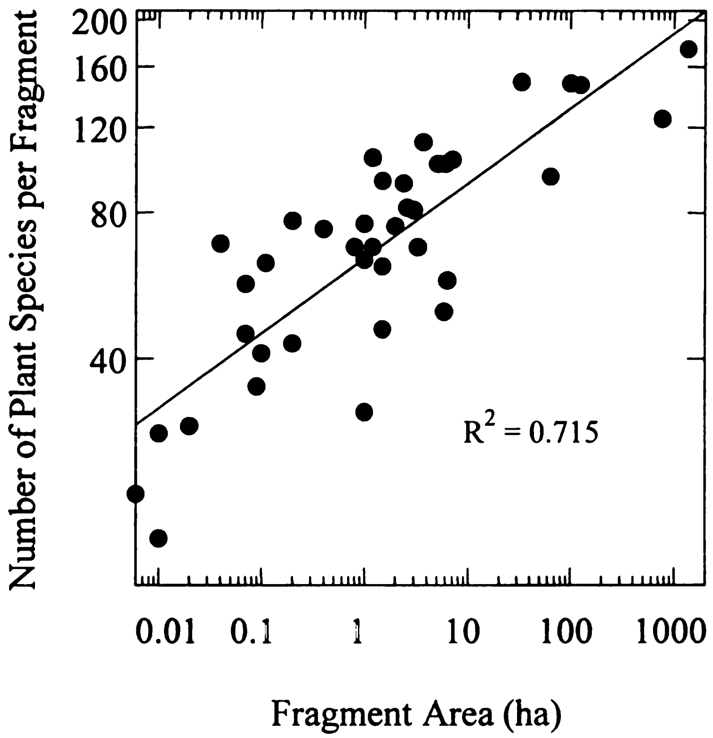

Figure 5.1: Species-area curve for Puerto Rican dry forest fragments. Note log scale.

Species richness increased significantly with fragment area. The power function was able to account for 71.5% of the variability in the relationship between species richness and area (Figure 5.1). The estimates of the parameters *c* and *z* were 69.3 and 0.127 for all fragments combines (Table 5.2). Parameter estimates based on a subset of the data are given in Table 5.2 below.

Table 5.2: The values of parameters *c* and *z* (and standard errors of the estimates) and the proportion of variance explained by the regression (R^2) obtained from species-area regressions for all fragments and various subsets of dry forest fragments, southwestern Puerto Rico.

	c	z	R^2
All Fragments	69.3 (3.6)	0.127 (0.013)	0.715
Relict Fragments	76.5 (5.6)	0.116 (0.019)	0.654
Fragments < 100 ha	68.6 (3.5)	0.143 (0.024)	0.557
Fragments < 10 ha	68.3 (3.4)	0.145 (0.031)	0.499
Fragments < 5 ha	70.3 (3.6)	0.166 (0.035)	0.547
Fragments < 1 ha	82.2 (11.3)	0.215 (0.059)	0.570
Fragments < 0.5 ha	94.3 (17.8)	0.263 (0.077)	0.572
Fragments + Guánica	51.4 (9.2)	0.259 (0.027)	0.689

Overall a sigmoid function yielded a poorer fit than did a power function. When S_{max} was not specified, the curve-fitting algorithm failed to converge – without “forcing” a fit, the sigmoid curve did not fit the data. If S_{max} was specified at 393, the explanatory power of the equation was high (0.727) for the fragments alone (Table 5.3). When S_{max} was set at 650, the curve-fitting algorithm failed to converge for the fragments alone, but was able to explain over 60% of the variance observed for the fragments and Guánica Forest combined (Table 5.3). The area in which half the species would be present (A50) varied greatly among estimates, ranging from 158 ha when S_{max} was set at 393 (for the fragments and Guánica Forest) to 7331 ha when S_{max} was set at 393 and the fragments alone were considered.

Table 5.3: Parameter estimates obtained using the sigmoid $\mathrm{Hill}_{\mathrm{Slope}}$ function (Lomolino 2000) for an array of Puerto Rican dry forest fragments alone and together with Guánica Forest, a 4000-ha reserve.

		Fragments	Fragments + Guánica Forest
$S_{max} = 393$	$\mathrm{Hill}_{\mathrm{Slope}}$	1.188	1.408
	A50	7330.9	158.3
	R^2	0.727	0.540
$S_{max} = 650$	$\mathrm{Hill}_{\mathrm{Slope}}$	--	1.359
	A50	--	2255.2
	R^2	--	0.603

Intra-fragment species-area curves also displayed an increase in species richness with area sampled in a pattern that was consistent with the power function. Estimates of the parameter *c* ranged from 2.64 to 10.92 (the lowest estimate, 2.03, was not statistically significant). Estimates of the parameter *z* ranged from 0.302 to 0.595 (Table 5.4). There was a positive correlation between the parameters *c* and *z* (Figure 5.2).

Species density (based on constant plot size, *sensu* Whittaker, 1975) was not significantly related to either fragment area or species richness, but was significantly related to fragment history (Table 5.5). There was also a significant interaction between fragment species richness and history.

Table 5.5: Least square mean estimates of species density (*sensu* Whittaker, 1975) based on fragment history in Puerto Rican dry forest fragments.

History	Adjusted Least Square Mean of Species Density	Standard Error	Number of Plots
Mixed†	30.36	1.96	41
Regrowth†	24.70	1.41	76
Relict†	20.69	0.44	230

† Fragments that have been forested continuously since 1936 are called Relict, those that have been non-forest at some point since 1936 are called Regrowth, and those that are a mosaic of both types are called Mixed. See text for a more complete explanation.

Table 5.4: Estimates of the parameters *c* and *z* of the species-area curve for intra-fragment sample curves of dry forest fragments, southwest Puerto Rico.

Site	c	z
1	8.98	0.418
2	5.42	0.435
3	6.76	0.414
4	6.23	0.443
5	6.93	0.392
6	10.68	0.328
7	9.56	0.389
8	7.97	0.393
9	2.64	0.302
10	9.08	0.384
11	8.04	0.401
12	8.38	0.405
13	5.37	0.465
14	6.00	0.479
15	8.15	0.366
16	3.65	0.461
17	3.79	0.449
18	10.65	0.359
19	8.46	0.337
20	3.43	0.486
21	7.69	0.384
22	4.07	0.440
23	5.78	0.432
24	2.86	0.455
25	10.92	0.353
26	7.15	0.406
27	3.57	0.538
28	3.66	0.538
29	2.03*	0.595
30	9.37	0.381
33	2.20	0.552
34	5.34	0.422
35	9.33	0.316
36	5.82	0.466
41	4.23	0.514
SEv†	2.84	0.560
DeF†	9.34	0.304
ScF†	1.94	0.452

* estimate not significant ($p < 0.0816$).

† Reference plots within Guánica Forest: SEv = Semi-Evergreen Forest, DeF = Deciduous Forest, ScF = Scrub Forest.

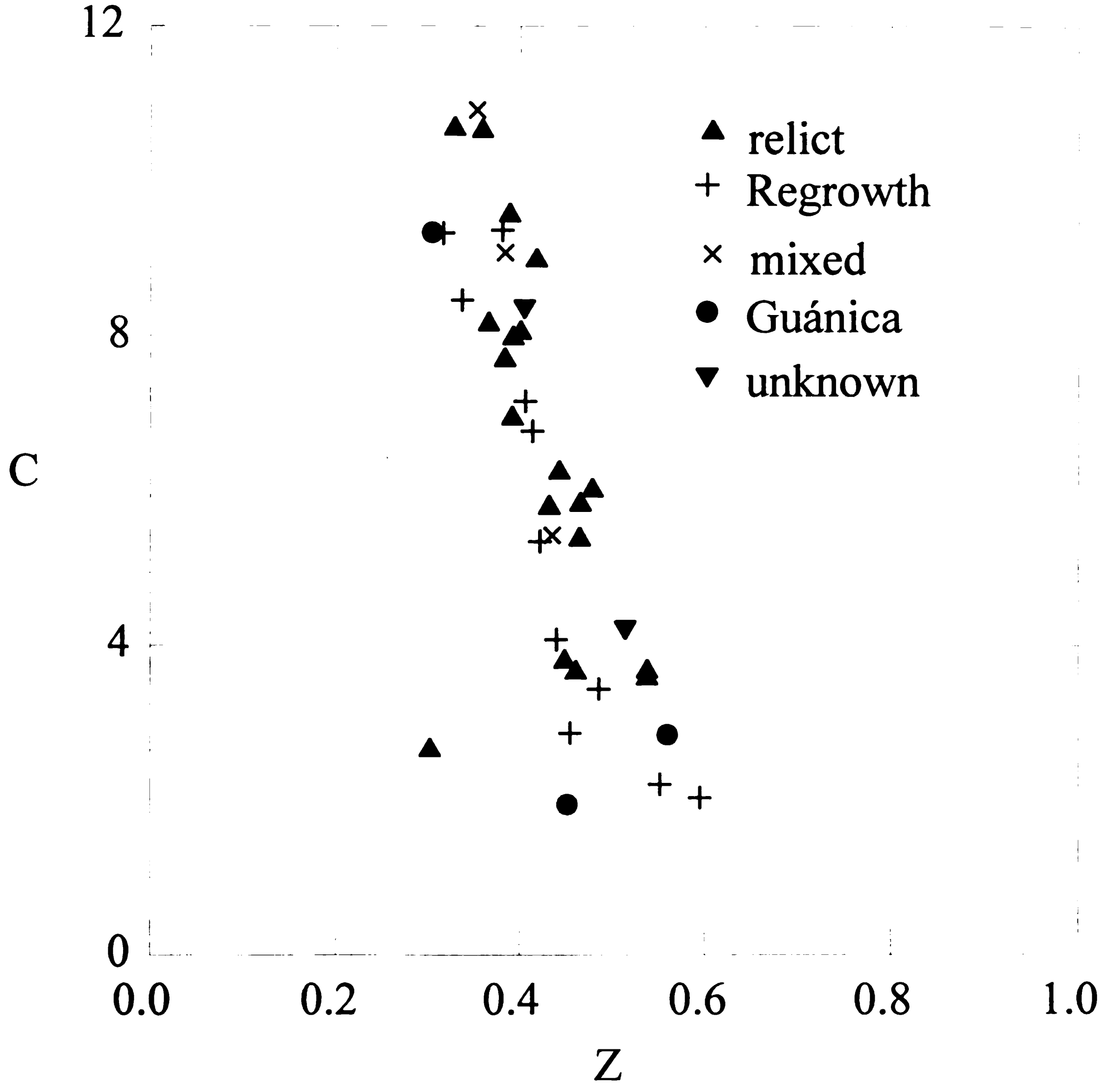

Figure 5.2: Estimates of the fitted parameters *c* and *z* of intra-fragment species-area curves of dry forest fragments in southwestern Puerto Rico. Species-area curves were modeled using the power function $S = cA^z$. Correlation coefficient r = 0.564 for all data, and 0.776 if the outlier, Site 9, is excluded.

Discussion

The evidence suggests that, for fragments larger than 1 ha, the relationship between species richness and fragment area was fairly consistent across the range of subsets of the fragment array. Although a small island effect (SIE) was observed for fragments smaller than 1 ha, in contrast to the expectations of the SIE (which predicts a fairly flat species-area relationship in very small sites; see Lomolino 2000), the slope of the species-area curve was steeper among the small fragments than it was for the full array of fragments.

On the surface this pattern among the small fragments is more in keeping with the predictions of He and Legendre (1996) that smaller fragments will have a steeper slope because they are prone to lose species more quickly. This will result in a steeper species-area curve. Closer examination of the data fails to support this interpretation. While the slope parameter (z) is steeper for the small fragments (those < 1 ha in size) than it is for the system as a whole, c is also larger for these small fragments. Thus, it would appear that the small fragments have more species per unit area than does the system as a whole.

It is reasonable, because of historical factors, to expect the smallest fragments to have a greater species density than larger ones. In the case of Regrowth fragments, since successional dry forests on abandoned agricultural land are species-poor (Molina Colón 1998) and there was no significant relationship between species richness and area, it would appear that second growth adds species slowly. The basic set of species present in Regrowth fragments is already present in small fragments. Small Relict fragments also appear to have the basic components of the mature dry forest communities (see Chapter 7). Large areas of species-poor Regrowth may cause the slope of the species-area curve to be flatter than it would otherwise be. Comparable phenomena are absent from small fragments regardless of their history.

Relict fragments had a flatter species-area curve than did the other subsets of fragments. The *z*-value, 0.116 is close to the value of 0.1 that is expected for samples drawn from continuous habitat (Rosenzweig 1995) and the *c*-value of 76.5 is second only to that of the group of fragments smaller than 0.5 ha. This may be the consequence of either less "relaxation" in Relict fragments, or undersampling in large fragments. Relict fragments may have fewer species and thus may resemble samples taken from continuous habitat. Alternatively, the flatness of the curve could be explained by under-sampling in the largest fragments, which could reduce the overall rate at which species are added, and so depress the entire regression.

Including Guánica Forest in the regression led to a large increase in the estimate of the slope parameter *z* from 0.127 to 0.259, and a decrease in the estimate of the parameter *c*, from 69.3 to 51.4. The estimate of *z* is almost identical with the 'canonical' value of 0.26 (Preston 1962). This suggests that the overall species-area curve is a sigmoid (which seems to be the overall consensus on the true form of species-area curves; Leitner and Rosenzweig 1997, Rosenzweig and Ziv 1999, Lomolino 2000, Lomolino and Weiser 2001). Small fragments (those below 1 ha in area) and large fragments have steeper species-area curves than do intermediate-sized areas.

Despite this fact, use of the sigmoidal $\mathrm{Hill}_{\mathrm{Slope}}$ function as suggested by Lomolino (2000) did not improve the overall regression. When used in the basic three-parameter form, the curve-fitting algorithm failed to converge and a regression could not be fitted to the data. Using the published species richness of 650 for Guánica Forest (Figueroa Colon

1996) or the observed species total of 393 are both unsatisfactory since neither figure reflects the total potential species pool. There are species found within the dry forest zone (and which are thus part of the total species pool) which are not present in Guánica Forest (see Chapter 7) and there are species recorded for Guánica Forest that are not part of the species-pool available to the fragment; these include mangrove species (fragments were, by definition, non-mangrove) and the more mesic species which have been recorded in sink holes (Farnsworth 1993), a habitat that was not sampled in any of the fragments.

The intra-fragment species-area curves were steeper than those usually observed for samples drawn from continuous habitat. Several explanations may be proposed to address this issue. Species-area curves were constructed from scattered, rather than contiguous, plots. It has been shown (*e.g.*, Rosenzweig 1995) that scattered plots tend to accumulate species more quickly than do contiguous plots. This is a reasonable expectation given that dry forest trees are clumped (Hubbell 1979); plots are expected to show spatial autocorrelation. Thus, scattered plots are more likely to pick up new species than are contiguous plots. In addition, these are very small samples. He and Legendre (1996) showed that small samples behaved differently, and yielded different estimates of the parameters c and z than did larger plots (when both were drawn from the same data).

Leitner and Rosenzweig (1997) found a positive relationship between c and z in simulated data sets. However, this relationship was found among samples drawn from species pools of different sizes. This was probably a consequence of the fact that both c and z scaled positively with the size of the source pool.

The observed pattern does not fit into most of the existent theory regarding the construction of communities with regards to species richness and species accumulation. As Whittaker *et al.* (2001) pointed out, if a factor does not vary consistently with species richness using equal-sized plots, then that factor cannot be a driver of species diversity in that context. By extension, factors that drive species richness should be observable at a local scale.

The observed patterns of *c*- and *z*-values could be best described as being 'complementary'. Sites that have higher *c*-values have lower slope parameters (*z*), while sites that have lower *c*-values have higher *z*-values. This pattern means that fragments either had high species richness or that species were rapidly added between plots – in other words, fragments either had high α-diversity or high β-diversity (*sensu* Whittaker 1975), not both. This is a reasonable conclusion if these fragments draw upon a pool of common species that account for the majority of all individuals. For the most part, diversity is driven by rare species, while sampling is most likely to encounter common species. Collectors curves compiled during the course of data collection appeared to level well before all species in the fragment were sampled. Murphy and Lugo (1986) observed a similar situation in Guánica Forest where their species-area curve approached a plateau after only 34 tree species were recorded.

Scheiner *et al.* (2000) discussed the importance of knowing the form of species-area curves through space – whether the curves are parallel or they intersect at some point has a major influence on the relationship between species richness and productivity, and is likely to affect other such relationships. Many of these curves intersect even within the area sampled. Thus, correlates with species richness are unlikely to be scale invariant, and functional relationships may well differ among fragments.

No relationship was observed between per-plot species richness (species density, *sensu* Whittaker, 1975) and either fragment area or species richness. The absence of such a relationship suggests that fragment species richness is not a function of species density. Species richness at the plot level is a function of fragment history. Examination of the least square means shows that Relict fragments were the most species poor (on a per plot basis) and Mixed fragments were the most species-rich. The difference in effect size between these groups is large. Mixed fragments had almost 50% more species per plot than did Relict fragments, despite the fact that Relict fragments on average had the highest species richness. This differs substantially from what Ross *et al.* (2002) found in Australian fragments. Their study was one of the few to look at species density (*sensu* Whittaker, 1975) in forest fragments of varying age. Contrary to the findings of this study, Ross *et al.* (2002) found that species density declined as fragments aged, especially when they were subject to disturbance (mostly fire) and invasion by exotic species.

This relationship suggests that disturbance is the real driver of species density (*sensu* Whittaker, 1975). This agrees with the predictions of the intermediate disturbance hypothesis (Connell 1978) and with Dunevitz's (1985) findings in Guánica Forest. As long as rootstocks remain in place, dry forest recovers rapidly from cutting, and the species that were present before cutting remain dominant (Ewel 1980, Molina Colón 1998). Once they have been eliminated, succession tends to be much slower and involves species that can establish from seed. These two processes involve different source pools – one, the trees that persist (Bond and Midgley 2001) and the other, species that establish from seed. In Mixed fragments, both source pools are present and plots are thus likely to be more species-rich. Although it may be suggested that Relict fragments are more species-poor because of the inclusion of several 'coastal' fragments that have very few species per plot, these account for only a small proportion of all Relict fragments and omitting them does not materially alter the results.

Taken together, these findings suggested that local (plot) species richness was not the driver of fragment species richness. Samples taken from continuous habitat yield species-area curves with flatter slopes than do similarly sized islands. Rosenzweig (1995) suggested than this was due to the presence of "sink species" in the samples drawn from continuous habitat. "Sink species" are species that are present in the sample because they are present in the large area of habitat that the continuous habitat provides; they would not be able to persist in an island the size of the area sampled from the continuous habitat. These species are only present in larger islands. Species richness increases more quickly with island area than it does in similarly sized mainland samples because certain species will be present in *samples* that are smaller than the minimum *island* size in which they can persist. If this is the case, then the species density should be higher in larger sites, so as to compensate for the flatter slope of the species-area curve, a process comparable to the 'mass effect' of Shmida and Wilson (1985).

In this system, fragment species richness appears to be a function of turnover between plots (β-diversity, *sensu* Whittaker, 1975) and not of 'point' species richness (α-diversity, *sensu* Whittaker, 1975). Whether this is caused by resource heterogeneity, negative density dependence in recruitment or disturbance history is not something that this study can discern, but it is clear that heterogeneity and not local species richness is the main driver of species richness.

On the other hand, is there any *a priori* reason to assume that species density should be a predictor of fragment species richness? Hubbell and colleagues (Hubbell *et al.* 1999, Hubbell 2001) suggested that local factors do not drive species richness. Instead, it was suggested that dispersal limitation is one of the key factors in the maintenance of diversity in tropical forest communities. Overall species richness (what Hubbell, 2001 calls 'metacommunity' species richness) is driven by local-scale differences in species composition. If this is the case, then Whittaker *et al.*'s (2001) assumption that plot species richness should drive site species richness may be questionable.

Summary

1) Fragment species richness was a function of fragment area and fragment history.
2) Inter-fragment species-area curves were better fit by a power function (the Arrhenius equation) than by a sigmoid function (the $\text{Hill}_{\text{Slope}}$ function).
3) A small-island effect (SIE) was observable among fragments smaller than 1 ha.
4) Inclusion of Guánica Forest into the species-area curve altered the parameters of the relationship but did not worsen the fit of the relationship; Guánica Forest has a larger range of habitat-types than did the fragments, and so would be expected to have a higher β-diversity than did the fragments.
5) The Arrhenius function explained 71.5% of the variance in the overall inter-fragment species-area curve and 65.4% of the variance in the Relict fragment species-area

curve; Regrowth fragments did not show a significant relationship between species-richness and area using either a power function or a linear regression.

6) Mixed fragments had the highest species density (*sensu* Whittaker, 1975) and Relict fragments had the lowest; there was no relationship between species density and fragment species richness.
7) There was a significant negative correlation between the parameters of the Arrhenius equation (c and z) in intra-fragment species-area curves.

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CHAPTER 6: PLANT SPECIES RESPONSES TO LONG-TERM FRAGMENTATION IN PUERTO RICAN DRY FOREST LANDSCAPE

Introduction

In studies of habitat fragmentation, species richness and diversity indices are among the primary descriptors of community patterns. However well these summary patterns describe the patterns of species distribution, they remain summary patterns, and can hide as much as they reveal. Community patterns are made up of individuals and species. The way these species (and the individuals that make up these species) distribute themselves on the landscape is what structures a community and drives community dynamics.

The existence of a trade-off between competitive ability and dispersal ability among plants is one of the basic features of models which attempt to explain coexistence in competitive communities. Species that are better competitors are likely to be locally dominant. Hubbell (2001) has shown that, in general, space is a limiting resource that is fully used. For a new individual to establish itself, a space must become available. Poorer competitors are able to survive in the community by being better dispersers. When a space becomes available, a superior disperser is more likely to find that space and become established. Jennings *et al.* (2001) and Vandermeer *et al.* (2001) have suggested that most competition among trees occurs at the seedling stage – it is difficult for a seedling to displace an adult tree regardless of its competitive advantage. Models have shown (Chesson and Warner 1981, Chesson 1986) that a trade-off between competitive ability and dispersal ability is adequate to allow coexistence over long periods of time. Hubbell (2001) has shown that even without that trade-off, the simple fact of dispersal limitation can allow for extremely long extinction times in local communities comprising a few thousand individuals.

Tilman and colleagues (Tilman *et al.* 1994, Tilman *et al.* 1997) have shown that, given the existence of a competition-colonization trade-off, dominant species are at risk in fragmented landscapes because they are less able to recolonize fragments from which they have gone extinct. Surprisingly, these models predict that weedy species will gain an advantage in a fragmented landscape even in the absence of further disturbance within the fragments.

The relationship between abundance and range is one of the fundamental relationships in macroecology (Gaston *et al.* 1997). Locally abundant species tend to have wider geographic ranges than do less abundant species. On local scales, where dispersal limitation is not likely to be a major factor, local dominance hierarchies are likely to be repeated across the landscape (Hubbell 2001). Thus, locally abundant species are likely to be superior competitors and are likely to be more widely dispersed geographically. However, because dominant species are likely to be relatively poor dispersers, they are less likely to recolonize disturbed areas.

Seed dispersal characteristics are likely to be important with regards to what species are able to colonize regrowth. If other things (such as dispersal syndrome) are controlled for, one would expect that small seeds would have a higher probability of being dispersed into a new site than would large seeds. On the other hand, large seeds are likely to have more reserves, which may be useful in establishing in new habitats. This may be especially relevant in seasonally dry areas, since seedlings need to have access to soil moisture in order to survive the dry season. Leishman and Westoby (1994) found that large seeds had an advantage in establishing under conditions of low soil moisture – it seems probable that this would also be true for surviving low soil moisture in the first dry season to which a seedling is exposed.

Objectives

1) To determine whether there is a correlation between abundance of species in the reference community (Guánica Forest) and their geographic range;
2) To determine whether there is a relationship between local abundance in Guánica Forest and frequency in sample plots within Guánica Forest;
3) To determine whether there is a relationship between local abundance within Guánica Forest and the number of fragments within which a species occurs;
4) To determine whether there are differences in the distribution of species that are locally abundant in Guánica Forest and species that are present in most of the fragments in terms of the drivers of their presence in fragments of differing species richness and history;
5) To determine whether there are differences in seed size among fragments with different disturbance histories;
6) To determine whether there is a difference in the abundance of exotic species among fragments with different disturbance histories.

Methods

Inventories were carried out in a total of 39 dry forest fragments as outlined in Chapter 2. Species recorded in a total of 19 25-m^2 plots in Guánica Forest were used to examine differences in the distribution of forest species in continuous and fragmented Puerto Rican dry forest. Each species present was assigned a Range score based on its biogeographic distribution (Liogier 1985, 1988, 1994, 1995, 1997; see Table 6.1).

Table 6.1: Criteria used to assign a Range score to Puerto Rican dry forest plant species

Score	Range
1	Endemic to Puerto Rico and adjacent islands.
2	Puerto Rico plus Hispaniola and the Virgin Islands.
3	Insular Caribbean (including the Bahamas and offshore islands administered by Venezuela).
4	Caribbean and either Florida, Central American or South America.
5	Tropical America (present in both Central American and South America).
6	Pantropical or extra-tropical.

Mean abundance was calculated for each species sampled in Guánica Forest on the basis of plots where the species was present, not from total area sampled. Frequency was calculated as the number of plots in Guánica Forest where the species was present. Incidence was calculated as the number of fragments where the species was present.

Distribution profiles were constructed for each of the five most abundant species and the five species with the highest Incidence with presence or absence plotted against species richness. LOWESS methods (Cleveland 1979, Cleveland and Devlin 1988) were used to fit the curves.

Seed mass (in mg) was obtained from Castilleja (1991) for each of 45 common tree species. These were grouped into three categories: small (0.1-20 mg), medium (20-

60 mg) and large (60-473 mg) seeds. The proportion of small, medium and large seeded species was compared among fragments by site history. For each of these 45 species, the number of fragments in which it was present (Incidence) was graphed against seed mass.

The mean number of individuals of exotic species per 25-m^2 plot was calculated on a per-site basis. All grasses except *Lasiascis divaricata* (L.) Hitch. were included, since most grasses were lumped into three morphospecies and were not identified to species. Not all grasses are exotic, but the majority of pasture grasses are exotics, and these include almost all grasses likely to be found in the fragments except *L. divaricata.*

Results

Range-Abundance-Incidence Patterns

Frequency-Abundance

There is a positive relationship between Frequency (the number of reference plots in Guánica Forest in which a species occurred) and Mean Abundance (mean number of individuals per reference plot in Guánica Forest in which a species occurred; Pearson correlation = 0.678; a significant positive exponential relationship $R^2 = 0.738$), but this pattern is largely a consequence of three species (*Gymnanthes lucida*, *Croton humilis* L., and *C. discolor* Willd.) which had both high frequencies and very high mean abundances (Figure 6.1).

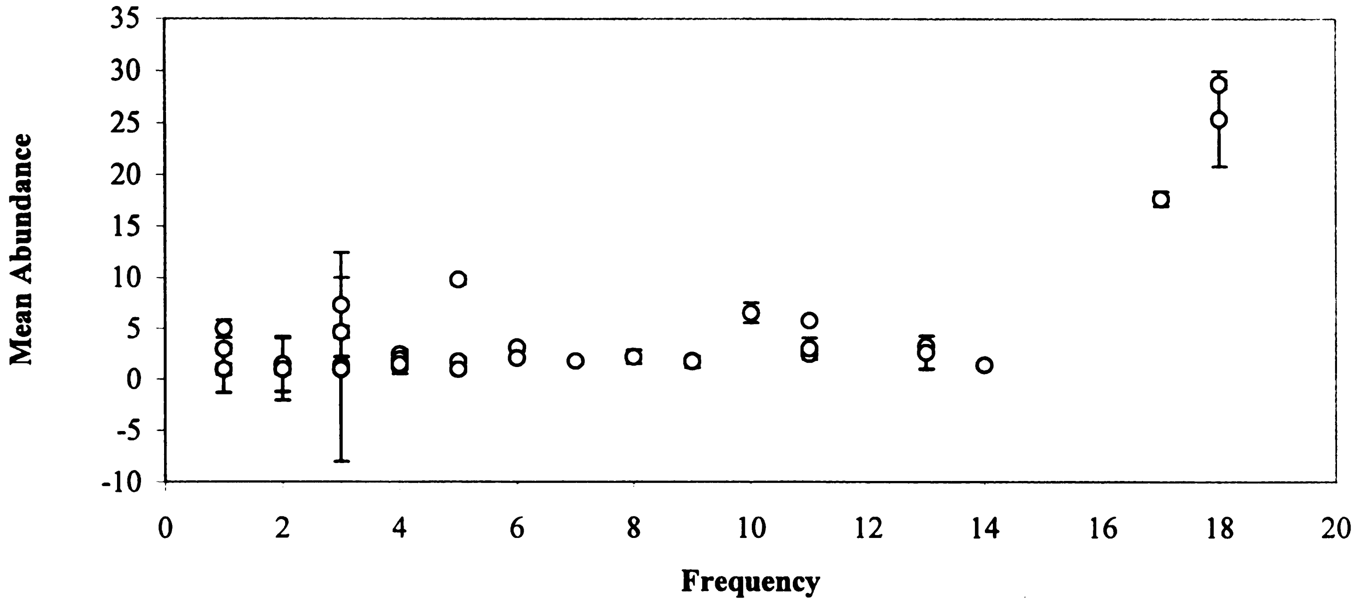


Figure 6.1: The relationship between Frequency (number of plots in Guánica Forest where a species occurs) and Mean Abundance (the mean number of individuals per 25 m^2 plot in Guánica Forest where the species is present) for Puerto Rican dry forest species. Data are presented as mean abundance ± 1 standard error.

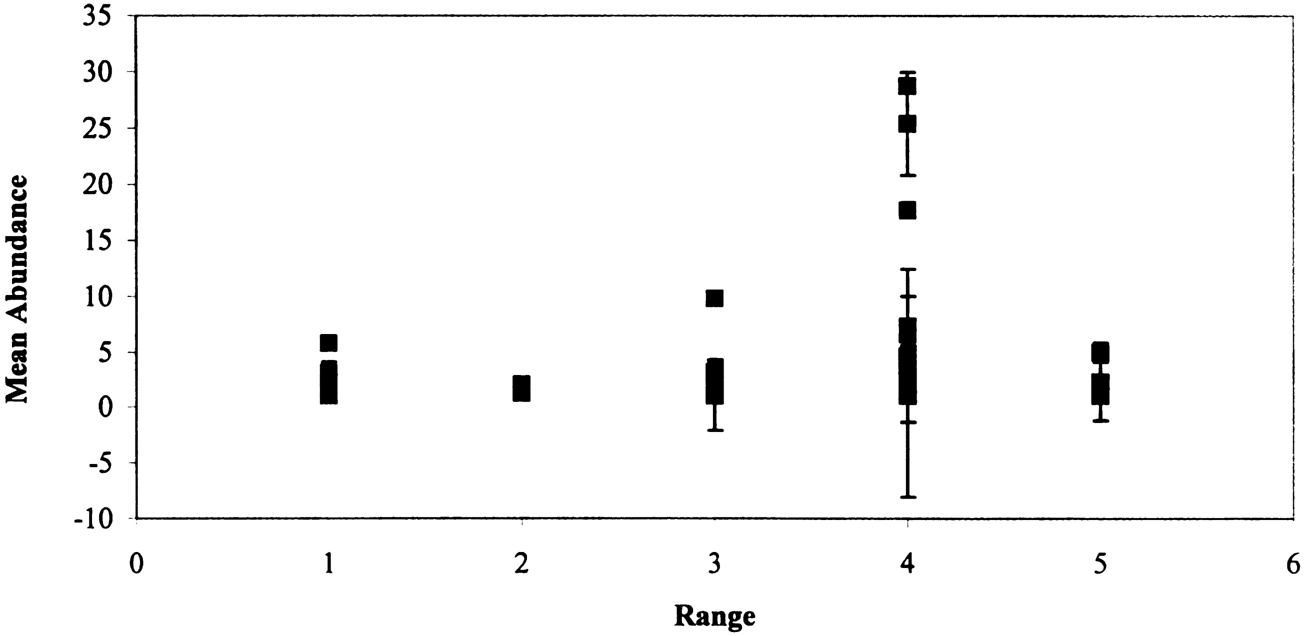


Figure 6.2: The relationship between Mean Abundance (the mean number of individuals per 25 m^2 plot in Guánica Forest where the species is present) and Range (the biogeographic breadth of the species distribution; see Table 6.1 for the meaning of the categories) for Puerto Rican dry forest species. Data are presented as mean abundance ± 1 standard error.

Range-Abundance

There was no statistically significant difference among the six classes (ANOVA, 45 d.f., $p < 0.543$). Species in Range class 4 (species found in the Caribbean and either Central America, South America or Florida) had the range of abundances in the reference plots in Guánica Forest (Figure 6.2).

Incidence-Abundance

There was little overall trend of abundance with increasing incidence. The species with the highest mean abundances were present in an intermediate number of fragments (Figure 6.3).

Species Profiles

The five species with the highest mean abundance in Guánica Forest (based on those reference plots in which they were present) were: *Gymnanthes lucida*, *Croton humilis*, *Eugenia foetida* Pers., *C. discolor* and *Erithalis fruticosa* L. LOWESS regressions yielded similarly shaped profiles for four of these five species; the curves had an intermediate peak at fragments of a species richness of about 60 species and then declined before increasing again (Figures 6.4a-d). The fifth species, *Erithalis fruticosa* had a monotonically increasing distribution profile, but was only predicted to occur in fragments with over 100 species (Figure 6.4e).

The five species with the highest incidences were *Bourreria succulenta*, *Distictis lactiflora* (Vahl) DC., *Lantana involucrata*, *Pilosocereus royenii*, and *Stigmaphyllon emarginatum* (Cav.) A. Juss. Their distribution profiles were approximately flat. The LOWESS regression predicted that these species would be present in all fragments (Figure 6.4f-j).

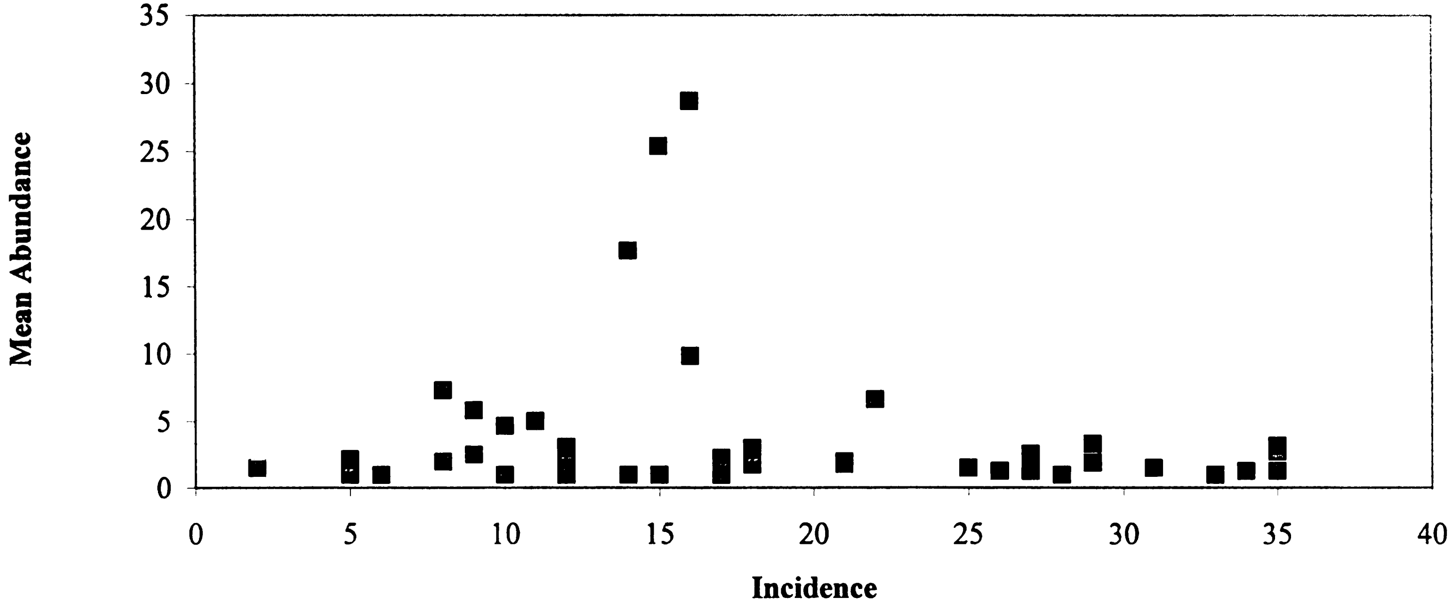
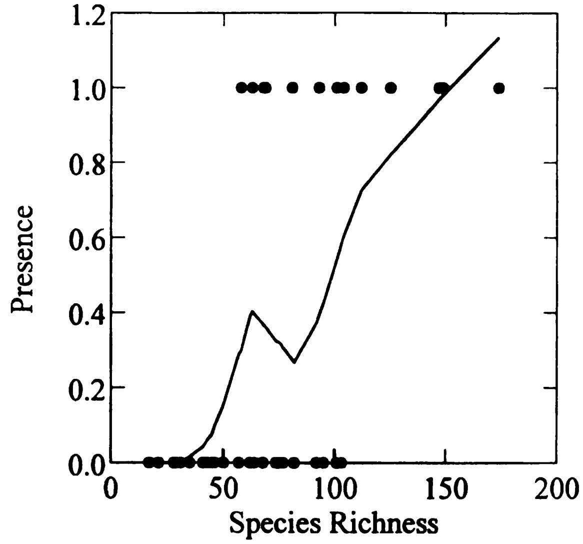
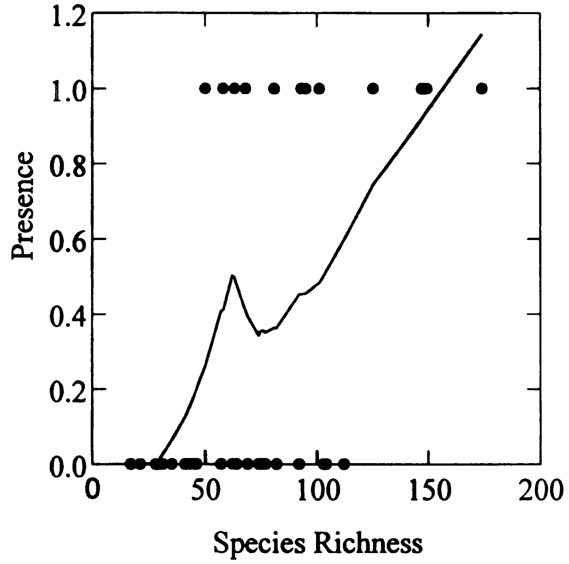


Figure 6.3: The relationship between Incidence (the number of fragments in which a species is present) and Mean Abundance (the mean number of individuals per 25 m^2 plot in Guánica Forest where the species is present) for Puerto Rican dry forest species.

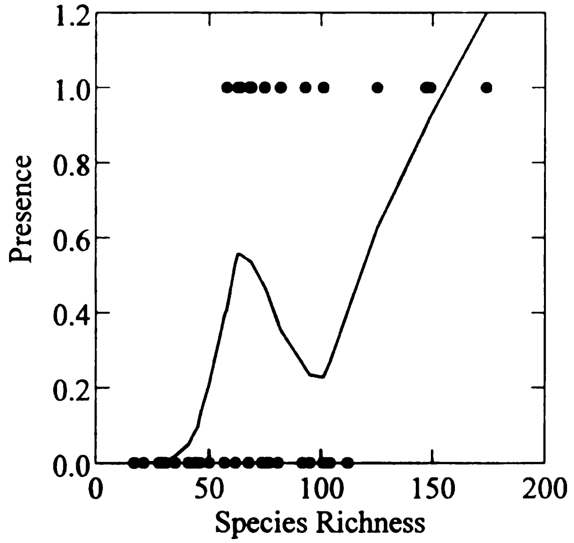


a: Abundance profile for *Gymnanthes lucida.*

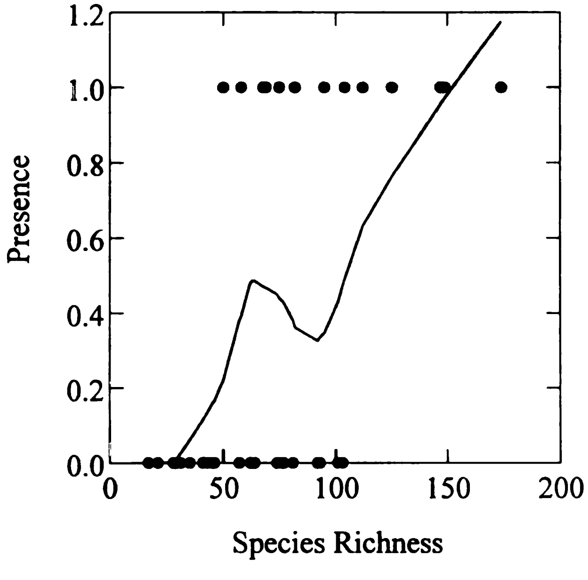


b: Abundance profile for *Croton humilis.*

Figure 6.4: Abundance Profiles (probability of the species being present as a function of fragment species richness) for dry forest species with the highest abundance in reference plots in Guánica Forest (**a-e**) or the highest incidence among the fragments (**f-j**).

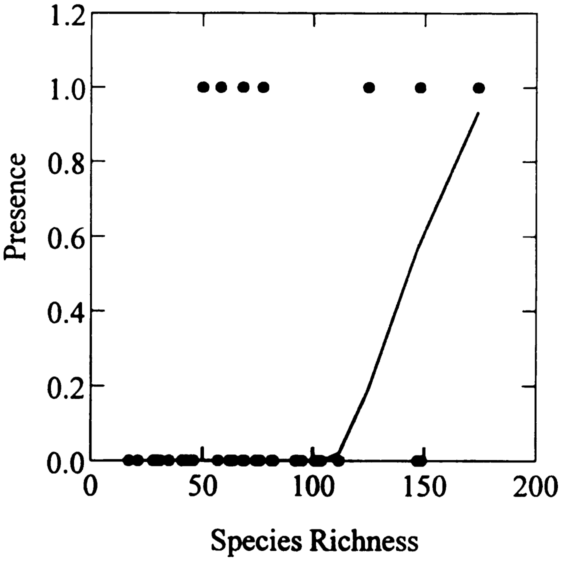


c: Abundance profile for *Eugenia foetida*.

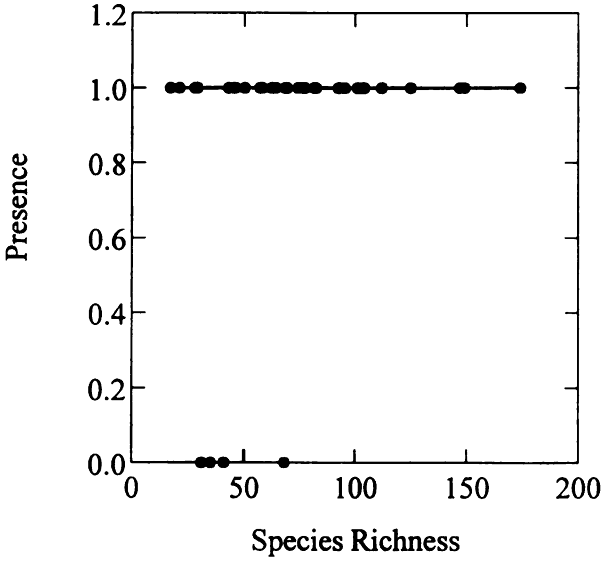


d: Abundance profile for *Croton discolor*.

Figure 6.4 (continued).

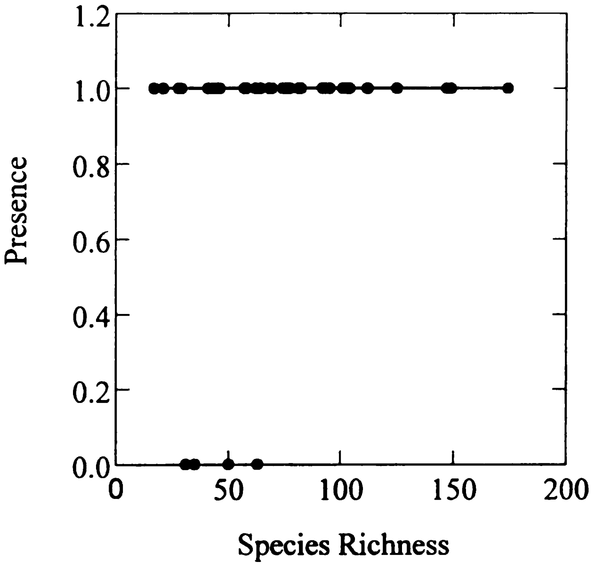


e: Abundance profile for *Erithalis fruticosa*.

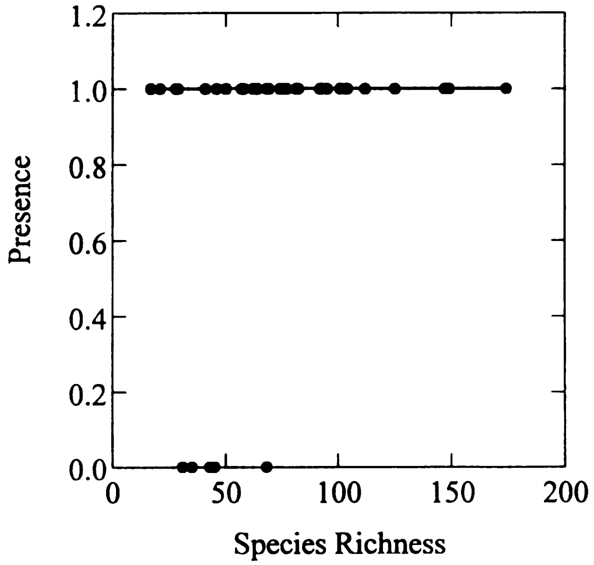


f: Abundance profile for *Bourreria succulenta*.

Figure 6.4 (continued).

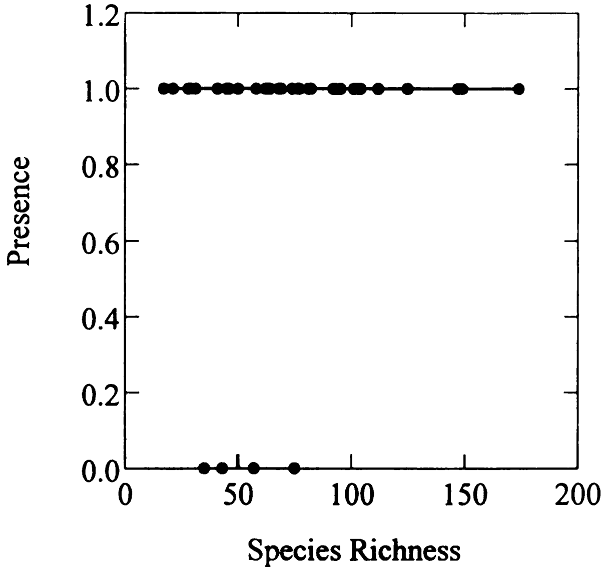


g: Abundance profile for *Distictis lactiflora.*

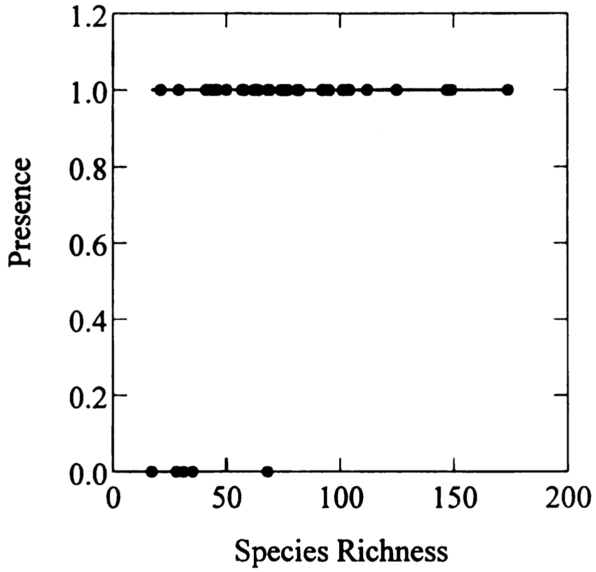


h: Abundance profile for *Lantana involucrata.*

Figure 6.4 (continued)



i: Abundance profile for *Pilosocereus royenii.*



j: Abundance profile for *Stigmaphyllon emarginatum.*

Figure 6.4 (continued).

Relative Abundance Profiles

Four of the five species with the highest abundances in Guánica Forest had small (0.21-0.59) positive Pearson product-moment correlations between their relative abundance in fragments and the species richness of the fragments. *Erithalis fruticosa* had a correlation of –0.06. The five species with highest incidences among fragments had small negative correlations (-0.08 to –0.14) between their relative abundance and the fragment species richness (Table 6.2).

Table 6.2: Pearson correlations between Abundance (among fragments) and Fragment Species Richness for each of 10 dry forest species in southwestern Puerto Rico.

	Species	Correlation with Species Richness
High Abundance	*Gymnanthes lucida*	0.227
	Croton humilis	0.585
	Eugenia foetida	0.428
	Croton discolor	0.211
	Erithalis fruticosa	-0.064
High Incidence	*Bourreria succulenta*	-0.144
	Distictis lactiflora	-0.084
	Stigmaphyllon emarginatum	-0.127
	Lantana involucrata	-0.142
	Pilosocereus royenii	-0.098

Site History

Four of the five species with the highest relative abundance in Guánica Forest showed a significant relationship between Incidence and fragment history (Table 6.3). *Erithalis fruticosa* was the sole exception. All of these species had a higher probability of occurrence in Relict than Regrowth fragments (Table 6.3).

Four of the five species with the highest Incidences showed a significant relationship between Incidence and fragment history (Table 6.3). The sole exception was

Table 6.3: The relationship between the distribution of selected dry forest plant species and fragment history in southwestern Puerto Rico

	Species	Pearson χ^2	probability	Relict Fragments: probability of occurrence	Regrowth Fragments: probability of occurrence
High Abundance	*Croton discolor*	13.306	< 0.001	73.7	6.3
	Croton humilis	12.781	0.002	63.2	6.3
	Erithalis fruticosa	1.293	0.524	26.3	12.5
	Eugenia foetida	9.381	0.009	63.2	12.5
	Gymnanthes lucida	12.106	0.002	63.2	6.3
High Incidence	*Bourreria succulenta*	2.061	0.357	94.7	81.3
	Distictis lactiflora	0.419	0.811	89.4	87.5
	Lantana involucrata	5.022	0.081	94.7	68.8
	Pilosocereus royenii	7.917	0.019	100	68.8
	Stigmaphyllon emarginatum	2.061	0.357	94.7	81.3

Pilosocereus royenii. All species showed a higher probability of being present in Relict than Regrowth fragments (Table 6.3). The Incidence of *Distictis lactiflora* showed almost no difference at all across fragment histories ($p < 0.811$), while *Lantana involucrata* showed the largest non-significant difference ($p < 0.081$).

Seed Mass

Most of the species in Relict and Mixed fragments were small seeded (0.1-20 mg). The number of species in each size class differed among fragments with different histories. Per fragment species totals differed with history for small seeded species (ANOVA, 36 d.f., $p < 0.0005$, $R^2 = 0.543$), medium seeded species (ANOVA, 36 d.f., $p < 0.0005$, $R^2 = 0.431$) and large seeded species (ANOVA, 36 d.f., $p < 0.001$, $R^2 = 0.321$). There was a high degree of collinearity between the distribution of the three seed sizes (small *vs.* medium, Person correlation $r = 0.809$, small *vs.* large, Pearson correlation $r = 0.814$, medium *vs.* large, Pearson correlation $r = 0.814$). As a result of this, use of an overall MANOVA was unwarranted. Overall this suggested that the real difference between sites was a function of overall species richness, which was supported by the fact that Relict and Mixed sites had very similar patterns, while the pattern in Regrowth fragments was different (Figure 6.5).

Since there were approximately twice as many small-seeded species as medium- or large-seeded species (22 small, 12 medium and 11 large seeded species), the pattern in the Relict and Mixed fragments did not differ from the expectation that the distribution of seed sizes among fragments was a random sample from the pool of species being tested ($\chi 2$ test, 3 d.f., $\alpha = 0.05$). The pattern in the Regrowth fragments was significantly

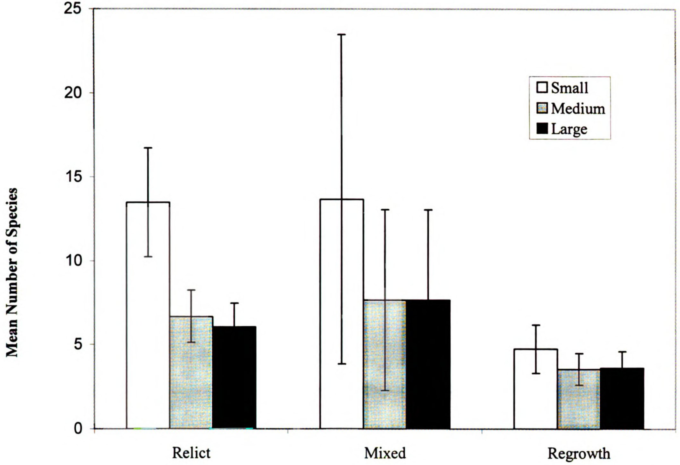


Figure 6.5: The number of species with small (0.1-20 mg), medium (20-60 mg), or large (60-473 mg) seeds in Puerto Rican dry forest fragments with different disturbance histories. Data are present as mean number of species per fragment ± 1 standard error.

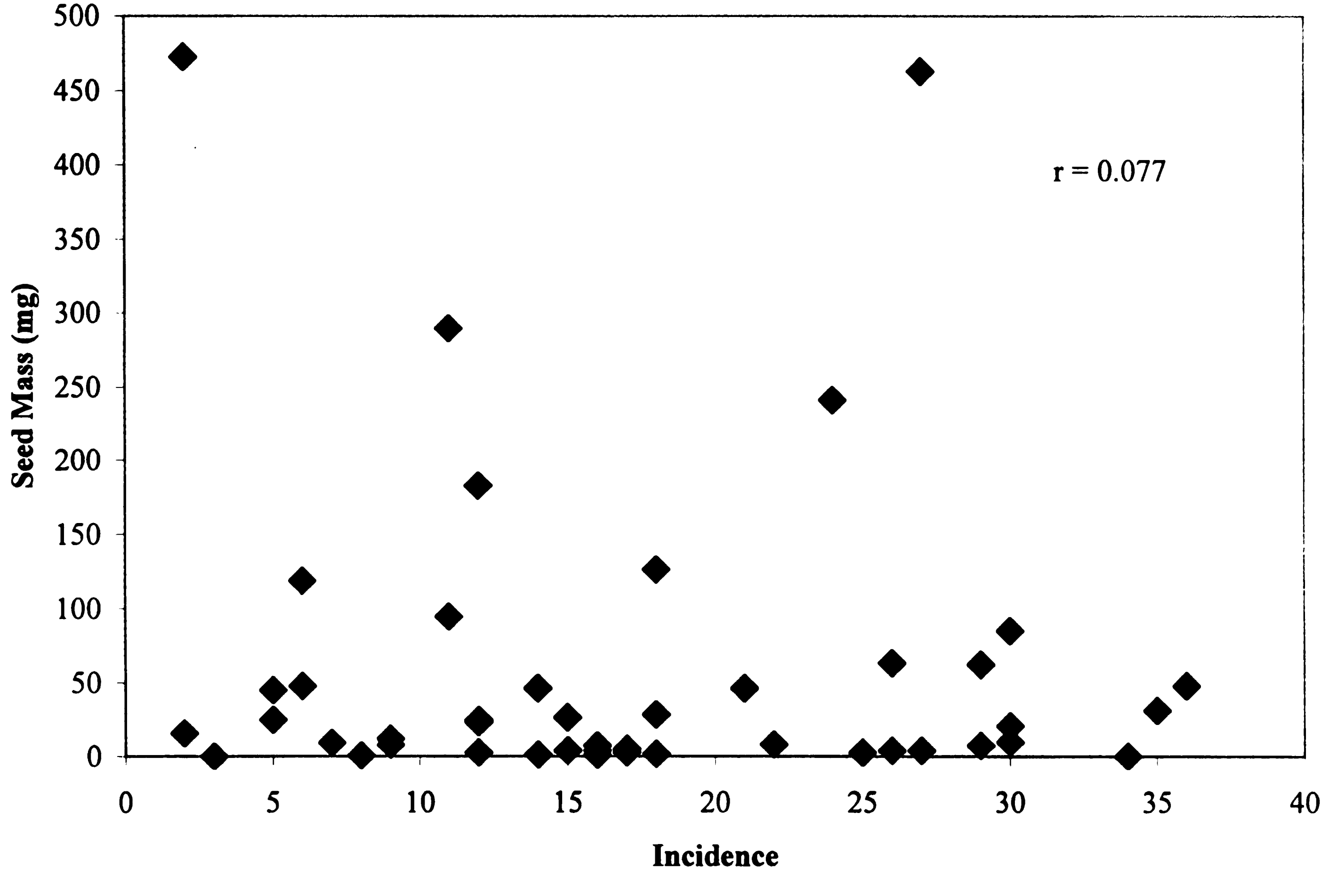


Figure 6.6: The relationship between seed mass and Incidence (the number of fragments in which a species is present) in dry forest fragments in southwestern Puerto Rico.

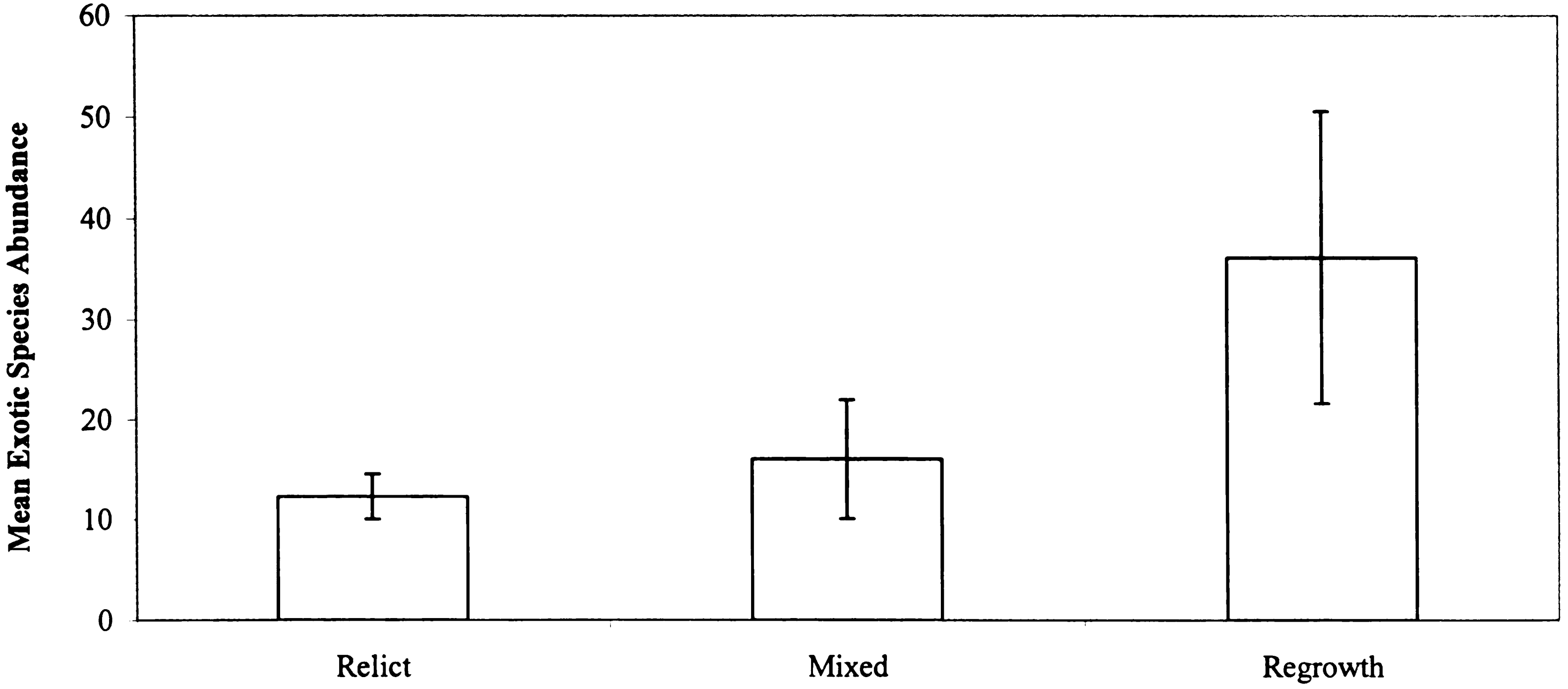


Figure 6.7: The mean number of exotic species per 25-m^2 plot in Puerto Rican dry forest fragments with different land-use histories. Data are presented as mean number of individuals per 25 m^2 plot ± 1 standard error. Relict fragments are those in which ≥ 75% of the fragment had supported forest cover continuously since 1936 ('old growth'), Regrowth fragments were ≤ 25% 'old growth', while Mixed fragments are 25-75% 'old growth' forest.

different from expectations. There were fewer small seeded species and more large-seeded species than would be expected by chance ($\chi 2$ test, 3 d.f., $\alpha = 0.05$). There was no apparent relationship between seed mass and Incidence (Figure 6.6).

Exotic Species Abundance

The abundance of exotic species (expressed in terms of the number of individuals per 25 m^2 plot) was higher in Regrowth fragments (36.1 ± 14.5 individuals per 25 m^2) and was lower in Mixed (16.0 ± 6.0 individuals per 25 m^2) and Relict (12.2 ± 2.2 individuals per 25 m^2) fragments (Figure 6.7). The overall relationship was not significant (ANOVA, 38 d.f., $p < 0.214$).

Discussion

One of the more general ecological patterns observable at large scales is that locally abundant species are more geographically widespread than locally uncommon species (Gaston *et al.* 1997). This pattern was not observed for these data. This may have been a consequence of the manner in which the geographical ranges were calculated. A species in Range Class 1 (Puerto Rican endemics) could conceivably occupy a larger range than a species in Range Class 2 (Puerto Rico, the Virgin Island and Hispaniola). For example, a Puerto Rican endemic that is distributed across the whole of the island (*e.g.*, *Thouinia striata*) may have a larger range geographically than a species which is present in Puerto Rico and Hispaniola but possesses a restricted distribution in both islands (*e.g.*, *Stahlia monosperma*). In addition, "whole community" measures may be inappropriate. Trends may have been stronger if analyses were restricted to more narrowly defined "guilds" or to more closely related taxa (*e.g.*, single families or genera).

Unlike the broader Range-Abundance pattern, the Range-Frequency pattern met these expectations, although this relationship was primarily driven by three species (*Gymnanthes lucida*, *Croton humilis*, *C. discolor*) with especially high mean abundances and frequencies. This pattern fits what Hubbell (2001) found in his analysis of tree species abundance in Peru; seven species showed a visible competitive advantage while the remaining species appeared competitively equivalent. On the other hand, some species, such as *Bursera simaruba* had a high frequency (it was present in nine out of 19 plots) but a low abundance (its abundance averaged 1.9 individuals per plot). At the other end of the spectrum *Erithalis fruticosa* had very high local abundances, but was present in only three plots. Species like this probably use a strategy much like what Bolker and Pacala (1999) called 'phalanx competition' – they are restricted to specific resource patches, but within those patches they can be very common and are able to out-compete other species (often by clonal spread).

The relationship between Abundance and Incidence also met theoretical expectations. Dominant species had intermediate Incidences. Four of the five dominant species were more likely to be present in Relict fragments than in Regrowth ones. Four of the five most widespread species showed no significant difference between their distributions in Relict, Mixed and Regrowth fragments. The species that are dominant in Guánica Forest (and to some extent in many of the Relict fragments) are absent from most of the Regrowth fragments. While it is impossible to disprove the hypothesis that these dominant species were not part of the pre-fragmentation community in the

Regrowth fragments, there is no *a priori* reason to assume that this should be the case. It seems more reasonable to assume that the absence of these species from Regrowth fragments is due to their failure to recolonize these areas as they reverted to forest; this pattern is expected given a trade-off between competitive ability and colonizing ability.

It is not surprising that *Gymnanthes lucida* is a poor colonizer given its dry, mechanically dispersed fruit (Castilleja 1991). It is more surprising that *Eugenia foetida* is a poor colonizer since it has small fleshy fruits. The fruit and seeds of *E. foetida* are smaller than those of *Bursera simaruba* and *Guaiacum officinale* L.; the fruits of both of these species are readily removed by frugivorous birds (Ricart Morales 1999). It is possible that it diverts relatively little energy to seed production, as might be expected if this species fits the profile of a resprouter rather than that of a reseeder (Kruger *et al.* 1997), or that seed production is limited by low pollinator visitation, pollen dilution (Aizen and Feinsinger 1994a, b) or limited disperser movement across the landscape. It is also possibly a consequence of low seed viability as a consequence of inbreeding depression.

The widespread species are likely to possess a suite of characters that helps them to colonize Regrowth fragments. Three of them are fleshy fruited, while the other two have winged fruit that are presumably wind dispersed. These species also do not appear to be forest dependent. *Bourreria succulenta* is an early successional species (Ray 1993, Ray and Brown 1995). *Pilosocereus royenii* is often found in open grassy areas (personal observation), while the vines *Stigmaphyllon emarginatum* and *Distictis lactiflora* can be found on fences and isolated trees (personal observations). The ability of these species to utilize the non-forested matrix probably plays a key role in their ability to colonize Regrowth.

While Regrowth fragments had a different distribution of seed sizes than did Relict and Mixed fragments, the prediction that there were more small-seeded species in Regrowth fragments was not supported. Instead, fewer small-seeded species were recorded in Regrowth fragments, possibly reflecting an advantage conferred by larger seeds in establishment in drier conditions. Seedlings establishing in abandoned pasture are likely to experience more severe dry season conditions than would seedlings establishing under tree cover. There was no clear pattern between seed mass and the number of fragments in which a species was present.

The higher proportion of exotic species in Regrowth relative to Relict fragments fits expectations. That the trend was not statistically significant is not surprising, since the standard errors were so large, especially for Regrowth fragments. While there is adequate light in the understory to allow germination (Castilleja 1991), it is likely that belowground competition (Coomes and Grubb 2000) will limit establishment in intact forest. It seems probable that trees will only recruit successfully when an established adult dies. The identity of the species that manages to capture an opening depends on the species that are present and able to get seeds into the opening – a gap poses no opportunity for a tree that produces no seed in the year that the gap appears. When a large area is opened for colonization and it is far from established forest patches, species that are nearby and that are able to produce large amounts of seed have an advantage in establishing *(e.g.*, Clark *et al.* 1999). Weedy species in general have an advantage, and exotic species are often weedy. Thus, it is reasonable to expect high exotic species abundances in Regrowth fragments. On the other hand, some exotic species are able to invade intact forest fragments; *Oeceoclades maculata* (a terrestrial African orchid) was primarily observed in 'high quality' Relict fragments.

Conclusions

Species are the drivers of community patterns. History is an important driver of the distribution of individual species. While many species appear to be able to readily colonize Regrowth forest, the typical community dominants are not among them. Abandoned agricultural land and young regrowth forest are widespread on the landscape. Any species that is able to exploit this habitat is likely to be abundant on the landscape, and thus, is likely to be an important component of the seed rain into newly available habitat. This study did not address the question of seed rain and species dynamics, but it seems reasonable to conclude that widespread, readily dispersed species are not only likely to be common in disturbed areas; they are also likely to form a disproportionate amount of the seed rain into undisturbed areas (see Janzen 1983).

If the dominants are unable to colonize Regrowth, it may be necessary to reintroduce them. It remains unclear as to whether *Leucaena leucocephala* hinders the establishment of native species or whether the native species are simply unable to disperse into regrowth dominated by *L. leucocephala*. In the moist forest zone of Puerto Rico, *L. leucocephala* was the best 'nurse crop' for native tree species among various exotic plantation species used for reforestation (Lamb *et al.* 1997). If it actually inhibits the establishment of native species in the dry zone, then it is probably a function of belowground competition. On the other hand, it may simply be that seed dispersers are not attracted to the dry-fruited *L. leucocephala* or that, as a deciduous species it fails to produce enough shade to allow seedlings to survive the dry season.

Since Relict and Regrowth fragments differ in species composition, they are likely to differ in their role in the conservation of the native biota. Given these differences, it is not safe to assume that the conservation value of a fragment is a simple function of its species richness. It is important to also incorporate information about the species composition of a fragment and how well it reflects the reference community. Chapter 7 addresses these concerns.

Summary

1) Species abundance correlated weakly with Range and Frequency, while the relationship with Incidence was complex.
2) The distribution of dominant species from Guánica Forest (the reference community) among fragments is a function of fragment history and species richness; dominant species are predominantly present in Relict fragments.
3) The distribution among fragments of the most widely distributed species correlated negatively with fragment species richness and was independent of fragment history (except in the case of *Pilosocereus royenii*).
4) The distribution of seed mass differed between Relict and Regrowth fragments; contrary to expectations, there were fewer small-seeded species in Regrowth fragments than in Relict fragments.
5) Exotic species had higher abundances in Regrowth fragments than in Relict or Mixed fragments but the difference was not statistically significant.

CHAPTER 7: THE CONSERVATION POTENTIAL OF DRY FOREST FRAGMENTS ON A TROPICAL LANDSCAPE

Introduction

Conservation in Fragmented Landscapes

Guánica Forest (Bosque Estatal de Guánica) occupies about 4% of the dry forest zone in southwestern Puerto Rico (Murphy *et al.* 1995); it is by far the largest area of protected dry forest on the island. This makes it the key resource for the conservation of dry forest biodiversity. Despite this fact, it cannot sustain the long-term survival of all dry forest species. While over 650 plant species have been recorded from Guánica Forest (Figueroa Colon 1996), several important elements of the dry forest biota are missing from this site. Of the 49 plant species formally recognized as threatened or endangered by the U.S. Fish and Wildlife Service, 13 have been recorded from dry forest habitats in southwestern Puerto Rico. Existing populations of only five of these species have been documented within Guánica Forest. Consequently, eight of these species depend entirely on habitat outside of Guánica Forest. Other protected areas including the Cabo Rojo National Wildlife Refuge and Laguna Cartagena National Wildlife Refuge provide critical habitat for some of these species (*e.g.*, *Aristida chaseae* and *A. portoricensis*; U.S. Fish and Wildlife Service 1994a, b), but others are entirely dependent on privately owned lands (*e.g.*, *Catesbaea melanocarpa* Krug & Urban in Urban; Silander 1999), which are often under considerable development pressure. Similar patterns are likely to exist for other rare species.

In addition to harboring species that may not be present in the main reserve, additional populations provide insurance against catastrophic events. While natural fires are rare events in this system, fires set by human agency are not infrequent in the dry season (personal observation) and occur regularly along roadsides in parts of Guánica Forest (M. Canals Mora, personal communication). Events like this can cause the extinction of a population (or a species if it is restricted to a single site).

Similarly, outbreaks of pests or pathogens tend to spread faster across contiguous populations. Populations broken into several isolates may have a better chance of surviving a disease outbreak (see Hess 1994, 1996). Breckon *et al.* (1998) and Breckon (2000) documented the apparent extirpation of *Opuntia repens* Bello (a species endemic to Puerto Rico and the Virgin Islands) from the offshore islands of Monito and Desecheo, presumably as a result of infestation by the cactus moth *Cactoblastis cactorum*. The same isolation that makes *O. repens* unlikely to recolonize these islands may also have stopped the outbreak from spreading to other populations.

Subdivided plant populations experience restricted gene flow (in the form of pollen and seed transfers among populations). This can affect the extinction probability of a small population. Inbreeding depression can reduce viability, seed production or growth rates as a consequence of the segregation of partially recessive lethal alleles. The loss of potentially adaptive variation in quantitative characters due to genetic drift can reduce the ability of the population to adapt to changing environmental conditions. The effects of new mildly deleterious mutations can accumulate and become fixed by genetic drift in small populations, thus lowering the overall viability of the population. The existence of forest fragments outside of Guánica Forest can play a role in reducing the degree of isolation experienced by populations in the main reserve. Fragments can encourage the movement of pollinators and seed dispersers across the landscape.

Adequate levels of seed and pollen movement among populations in Guánica Forest, the fragments, and perhaps the forests of the Cordillera Central, can ameliorate many of the aforementioned negative genetic consequences.

It is important to be able to assign a value to forest fragments for two main reasons: to identify valuable habitat that may be acquired for conservation purposes or for which conservation easements may be obtained, and to be able to determine whether or not a site proposed for development is important in a conservation context.

Forested lands outside of Guánica Forest are under the control of several different bodies and differ in the degree of protection afforded to them. Protected lands include public lands administered by the Puerto Rico Departamento de Recursos Naturales y Ambientales (DRNA) and the U.S. Fish and Wildlife Service (US FWS) and private lands under the control of the Fundación Puertoriqueña de Conservación (Puerto Rico Conservation Foundation). While other lands, including those under the control of government agencies and those in private hands, lack formal protection, many development activities are subject to laws and regulations that require a permitting process. This allows the government some measure of control over the fate of forest fragments on lands lacking formal protection.

Ideally, a conservation management plan for the whole landscape should be devised that protects enough natural habitat to ensure the long-term survival of all native species. In heavily deforested landscapes this option does not present itself; it is unlikely that enough habitat exists to ensure the survival of all species in the absence of management interventions. Instead of attempting to determine whether any given patch of habitat can ensure the long-term survival of any given species, the objective is one of identifying the remaining habitat patches which will make the largest possible contributions to the survival of as much as possible of the native biota. Most modern attempts to select optimal sets of reserves are based on the complementarity principle (Vane-Wright *et al.* 1991): the overall idea is that new reserves should be selected to bring in the maximum number of species not already present in existing reserves. The objective of determining a minimum set of reserves is that each (target) species should be present in at least a certain (predetermined) number of reserves. No method of site selection can be better than the information used in the selection process. However, since the resources employed in data collection are likely to originate from the same pool of funds that can be used for conservation it is imperative that the methods of assessing the value of potential conservation areas should maximize cost effectiveness.

What constitutes a valuable fragment?

While any fragment that preserves a viable population of a native species may be potentially valuable to the conservation of that species, valuable fragments should harbor viable populations of as many native species as possible, and should also preserve interactions between these species and the cycles of energy and nutrient flow through the system. More specifically there are three criteria that can be used to assess value.

1. <u>Conservation</u>: whether the species present are considered to be in need of protection.
2. <u>Representativity</u>: whether the species present are representative elements of the community from which they are (presumably) drawn.
3. <u>Connectivity</u>: where the site lies in proximity to other fragments, and its overall setting in the landscape (see Chapter 3).

Species richness is one of the most commonly used criteria for assessing conservation value (Dufrêne and Legendre 1997). The use of species richness poses some problems since species richness increases with area. Thus, this can amount to simply assigning conservation on the basis of fragment area. While this is not necessarily a bad criterion, it introduces potential confounding that should be acknowledged.

Species density (a measure of the number of species per unit area) would appear to compensate for the relationship between species and area. Sites that have more species per unit area than expected ("hotspots" as such) might be seen as important since they can protect more species in a given area than can less "species dense" sites. However, one must account for the fact that the relationship between species and area is non-linear (see Chapter 5 for a discussion of species-area curves). As a consequence, one must control for this in computing species density. Whittaker *et al.* (2001) recommends the use of fixed-area plots to measure species density because statistically normalized estimates of species richness tend to average the range of variability in the site, but it is precisely this 'summary' property of statistical prediction that makes this measure of species density appealing in this situation. The conservation value of a fragment is the product of these interactions. In addition, as mentioned in Chapter 5, there does not seem to be any compelling reason why overall fragment species richness should be a function of local species richness (α-diversity) – in fact, it is difficult to explain the species richness of Guánica Forest or any of the fragments without stressing the importance of habitat heterogeneity and β-diversity.

Measures of species richness are neutral with regards to the species involved. Metrics that regard species simply as numbers (*e.g.*, species area curve and diversity indices) mask the identity of the species involved. The presence of exotic species in a fragment can inflate the species richness and yet is likely to decrease, not increase, its conservation value (see Chapter 6).

An alternative to using a measure of species richness is to compare the species composition of the fragment to some standard list of species (*e.g.*, Webb 1989). Dufrêne and Legendre (1997) considered this a more satisfactory means of assessing conservation value. The actual species composition of the fragment is what is considered, and species not characteristic of the system (*e.g.*, exotics) can be discounted. One weakness of this method lies in the construction of the reference list; as Dufrêne and Legendre (1997) pointed out, "representativity" is a subjective concept and it requires that a "typical" or "pristine" example of the community be identified. If a reference sample can be identified, then (relatively) objective reference lists can be compiled through random sampling. This is less of a problem philosophically for adherents of the Zurich-Montpellier school, where relève selection requires the identification of a "typical" portion of the community.

This method, which values sites on the basis of how typical they are, can be complemented by searching fragments for less common elements of the community. The number of rare or endangered species present in a fragment can serve as a measure of its conservation value even if the site is not a typical example of the community. Kirkpatrick and Gilfedder (1995) found that sites that contained endangered species in Tasmania were not necessarily those with the highest biological integrity.

An alternate method of identifying sites of high conservation value would be to identify species that have high fidelity for valuable sites. Such indicator species could be used to identify valuable fragments. Indicators are suitable tools whenever the data are too complex to handle without aggregation (Müller *et al.* 2000). Indicator species can serve as 'flags' if vegetation descriptions are required as baseline elements in the preparation of permits for development activities. Unfortunately, the selection of indicators requires that some measure of conservation 'value' be made beforehand, thus making indicators sensitive to the biases inherent in the selection of the measure of 'value' selected.

Objectives

1) To develop methods to determine the conservation value of Puerto Rican dry forest fragments;
2) To evaluate the conservation potential of the studied dry forest fragments;
3) To designate and evaluate indicators of high quality dry forest fragments that can be used to prioritize conservation decisions.

Methods

Data Collection

Inventories were carried out in a total of 39 dry forest fragments in southwestern Puerto Rico. The selection of study sites and the methods of data collection are outlined in Chapter 2.

Species Richness/Species Density

Inter-site species-area curves were modeled by means of a power function of the form

$$S = cA^z$$

(Preston 1962, MacArthur and Wilson 1967) where S represents the species richness of the fragment, A represents the area of the fragment in hectares and c and z are fitted parameters. The parameters were estimated by maximum likelihood nonlinear regression of the untransformed data (See Chapter 5, Figure 5.1 and Table 5.1 for more details of the species-area relationship). Residuals of the regression were scaled relative to the value predicted by the regression via a χ^2 transformation

$$(\text{Observed} - \text{Expected})^2/(\text{Expected})$$

and were assigned a sign (positive or negative) based on whether the observed species richness was greater than or less than the predicted value. Values of the standardized residuals that were greater than 3.84 were considered to be significantly different from the predicted value (at the 0.05 level, based on a 1 degree of freedom χ^2 test). All analyses were carried out using Systat 9 (SPSS Inc., 1998).

As shown above, the relationship between species richness, S, and area, A, is nonlinear. If species density were calculated as S/A, it would decrease with area, and larger sites would necessarily have a lower species density than smaller sites. If the functional form of the relationship between S and A is accounted for, then the measure of species density becomes S/A^z which is c (since $S = cA^z$). Species densities were calculated for each fragment and fragments were ranked on the basis of species density.

Representativity

Reference lists were compiled based on the species composition of a total of 19 25 m^2 plots in three forest associations in Guánica Forest (see Chapter 2 for details). The species composition of each fragment was compared with reference lists complied from randomly sampled plots located in each of the three main forest associations present in Guánica Forest: Semi-Evergreen forest, Deciduous forest and Scrub Forest. See Table 2.1, Chapter 2 for sampling design. The reference lists for each association are presented in Table 7.1.

Species lists for all studied fragments were compared with these reference lists and the proportion of species in each reference list present in the fragment was calculated.

Table 7.1: Reference List of Representative Species sampled from Guánica Forest

Coastal Scrub	Deciduous Forest	Semi Evergreen Forest
Amyris elemifera	*Amyris elemifera*	*Amyris elemifera*
Antirhea acutata	*Antirhea acutata*	
Argythamnia spp.[1]	*Argythamnia* spp.[1]	*Argythamnia* spp.[1]
Ayenia insulaecola[2]		
Bernardia dichotoma		
Bourreria succulenta[3]	*Bourreria succulenta*[3]	*Bourreria succulenta*[3]
Bucida buceras	*Bucida buceras*	*Bucida buceras*
Bursera simaruba	*Bursera simaruba*	*Bursera simaruba*
	Canella winterana	
Capparis cynophallophora[4]		*Capparis cynophallophora*[4]
Capparis flexuosa		*Capparis flexuosa*
		Celosia nitida
		Chiococca alba[5]
Cissus trifoliata		*Cissus trifoliata*
	Coccoloba diversifolia	*Coccoloba diversifolia*
Coccoloba krugii	*Coccoloba krugii*	
	Coccoloba microstachya	*Coccoloba microstachya*
Colubrina arborescens		
Colubrina elliptica		*Colubrina elliptica*
Commelina elegans		*Commelina elegans*
Comocladia dodonaea	*Comocladia dodonaea*	
		Cordia rickseckeri
Crossopetalum rhacoma	*Crossopetalum rhacoma*	
		Crotalaria lotofolia
Croton betulinus		
Croton discolor	*Croton discolor*	
Croton humilis	*Croton humilis*	

Table 7.1: (continued).

Coastal Scrub	Deciduous Forest	Semi Evergreen Forest
	Distictis lactiflora	*Distictis lactiflora*
	Elaeodendron xylocarpum	
Erithalis fruticosa	*Erithalis fruticosa*	
		Erythroxylum areolatum
	Erythroxylum rotundifolium	
	Eugenia axillaris	
Eugenia foetida	*Eugenia foetida*	*Eugenia foetida*
Eugenia lingustrina		*Eugenia lingustrina*
Eugenia rhombea	*Eugenia rhombea*	*Eugenia rhombea*
Eugenia xerophytica	*Eugenia xerophytica*	
		Eugenia sp.
Exostema caribaeum[6]	*Exostema caribaeum*[6]	*Exostema caribaeum*[6]
Forestiera segregata	*Forestiera segregata*	
Grass sp.1		
Grass sp.3	Grass sp.3	Grass sp.3
Guaiacum sanctum		*Guaiacum sanctum*
Guettarda elliptica	*Guettarda elliptica*	
Guettarda krugii	*Guettarda krugii*	*Guettarda krugii*
Gymnanthes lucida	*Gymnanthes lucida*	*Gymnanthes lucida*
Heteropterys purpurea	*Heteropterys purpurea*	*Heteropterys purpurea*
Hibiscus phoeniceus		
	Hypelate trifoliata	
Ipomoea steudelii	*Ipomoea steudelii*	*Ipomoea steudelii*
Jacquinia berterii[7]	*Jacquinia berterii*[7]	
Jacquemontia cumanensis		*Jacquemontia cumanensis*
Krameria ixina		
Krugiodendron ferreum	*Krugiodendron ferreum*	*Krugiodendron ferreum*

Table 7.1: (continued).

Coastal Scrub	Deciduous Forest	Semi Evergreen Forest
Lantana involucrata	*Lantana involucrata*	
	Leptocereus quadricostatus	
Leucaena leucocephala		*Leucaena leucocephala*
		Macfaydena unguis-cati
Melocactus intortis		
Melochia tomentosa		
		Opuntia sp.
Orchid	*Orchid*	
		Passiflora suberosa
Phoradendron		
Pictetia aculeata	*Pictetia aculeata*	*Pictetia aculeata*
Pilosocereus royenii	*Pilosocereus royenii*	*Pilosocereus royenii*
Pisonia albida	*Pisonia albida*	*Pisonia albida*
		Pithecellobium unguis-cati
Plumeria alba		
Randia aculeata	*Randia aculeata*	
	T 012	T 012
Reynosia guama	*Reynosia guama*	
Reynosia uncinata	*Reynosia uncinata*	
		Samyda dodecandra
		Schaefferia frutescens
	Scleria lithosperma	
		Serjania polyphylla
	Sideroxylon obovatum	*Sideroxylon obovatum*
	Siphonoglossa sessilis[8]	
		Solanum americanum
		Heliotropium angiospermum

Table 7.1: (continued).

Coastal Scrub	Deciduous Forest	Semi Evergreen Forest
Stigmaphyllon emarginatum	*Stigmaphyllon emarginatum*	*Stigmaphyllon emarginatum*
Tabebuia heterophylla	*Tabebuia heterophylla*	*Tabebuia heterophylla*
Thouinia striata[9]	*Thouinia striata*[9]	*Thouinia striata*[9]
Tillandsia recurvata	*Tillandsia recurvata*	*Tillandsia recurvata*
Tournefortia microphylla		*Tournefortia microphylla*
	Tree (Myrtaceae)	
Turnera diffusa	*Turnera diffusa*	
	Vine sp.12	
	Vine sp.22	
	Vanilla spp.[10]	
Wedelia	*Wedelia*	
		Ziziphus reticulata

[1] *Argythamnia* spp. = *A. candicans* and *A. stahlii*; these species could not be readily distinguished in the field. Voucher specimens are overwhelmingly *A. candicans*, suggesting that most records are of this species

[2] Liogier (1988) spells this *A. insulicola.*

[3] Records of *Bourreria succulenta* may include *Cordia laevigata* (see Acevedo-Rodriguez 1996); voucher specimens suggest that most records are of *B. succulenta.*

[4] May include *Capparis indica.*

[5] May include *Chiococca parviflora.*

Table 7.1: (continued).

[6] Certain herbarium specimens at the University of Puerto Rico Herbarium, Rio Piedras, which were attributed to *Guettarda odorata* (= *G. parviflora* according to C. D. Adams, British Museum) are vegetatively similar to *Exostema caribaeum.* If these determinations are correct, then it is possible that some records of *E. caribaeum* may actually represent *G. parviflora.*

[7] Liogier (1995) stated that this should really be *J. berteroi* based on the fact that the species was named for Bertero.

[8] "R. A. Howard considers this species to be *Justicia*" (Acevedo-Rodriguez 1996)

[9] *Thouinia portoricensis* has been relegated to varietal status (*T. striata* var. *portoricensis*; Liogier 1988). While most of the individuals fit the description of *T. striata* var. *portoricensis*, others matched the description of *T. striata* var. *striata* or were intermediate between the two varieties. On the basis of the recorded geographic distribution of the two varieties I would expect to find *T. striata* var. *portoricensis* in the study area, but I do not feel confident enough to attribute varietal status to all material observed in the field.

[10] *Vanilla* spp. – most probably *V. barbellata* Reichenbach f. and *V. claviculata* (W. Wright) Swartz.

Rare and Endangered Species

A list of rare and endangered species was compiled from three published sources: the U.S. Fish and Wildlife Service list of threatened and endangered species (13 listed species and one candidate for listing; details available through the Internet at http://endangered.fws.gov/), a list of 27 threatened and endangered species present in Guánica Forest (Quevedo *et al.* 1990) and a list of 40 rare species compiled on the basis of herbarium records (Figueroa Colon and Woodbury 1996). Together these account for a total of 53 species that are either present in the study area or which have been recorded there at some time in the past (Table 7.2). The number of rare and endangered species was recorded for each of the 39 fragments for which complete species lists were compiled.

Indicator species

Incidence functions (*sensu* Diamond 1975) were constructed for the plant species present in each of the studied fragments. Fragments were grouped into seven classes on the basis of species richness with each class consisting of either five or six fragments. Species incidence was calculated for each species within each class; incidence was calculated as the proportion of sites in a class that were occupied by the species. Potential indicator species were selected on the basis of incidence. Species that were present in no more than 20% of the sites in each of the three least species-rich classes and that were present in not less than 80% of the two most species rich classes were designated as indicators of species-rich fragments. Fragments were scored in terms of the number of indicator species present.

Table 7.2: Rare and endangered plant species which are either present in the dry forest zone, southwestern Puerto Rico or have been recorded there in the past. The list was compiled on the basis of Federally listed endangered species, herbarium collections (Figueroa Colon and Woodbury 1996), or on their distribution in Guánica Forest (Quevedo *et al.* 1990).

Family	**U.S. Fish and Wildlife Service (Federally Listed)**[1]	**Figueroa Colon & Woodbury (1996)**	**Quevado *et al.* (1990)**
Malvaceae		*Abutilon commutatum*	*Abutilon commutatum*
Poaceae	*Aristida chaseae*	*Aristida chaseae*	
Poaceae	*Aristida portoricensis*		
Boraginaceae			*Bourreria virgata*
Cyperaceae		*Bulbostylis curassavica*	*Bulbostylis curassavica*
Cyperaceae			*Bulbostylis pauciflora*
Leguminosae		*Caesalpinia portoricensis*	
Rubiaceae	*Catesbaea melanocarpa*	*Catesbaea melanocarpa*	*Catesbaea melanocarpa*
Euphorbiaceae			*Chamaesyce cowellii*
Boraginaceae		*Cordia rupicola*[2]	*Cordia rupicola*[2]
Euphorbiaceae		*Croton nummulariifolia*	*Croton nummulariifolia*
Cyperaceae		*Cyperus urbanii*	
Leguminosae		*Dalea carthagenensis* var. *portoricensis*	*Dalea carthagenensis* var. *portoricensis*
Orchidaceae			*Encyclica krugii*[3]
Leguminosae		*Erythrina eggersii*	
Myrtaceae		*Eugenia bellonis*[4]	*Myrtus bellonis*[4]
Myrtaceae		*Eugenia boqueronensis*	
Myrtaceae		*Eugenia glabrata*	
Myrtaceae	*Eugenia woodburyana*	*Eugenia woodburyana*	*Eugenia woodburyana*
Asteraceae		*Eupatorium oteroi*	
Zygophyllaceae			*Guaiacum sanctum*
Nyctaginaceae			*Guapira discolor*
Cactaceae	*Harrisia portoricensis*	*Harrisia portoricensis*	
Boraginaceae		*Heliotropium guanicense*	

Table 7.2 (continued).

Family	**U.S. Fish and Wildlife Service (Federally Listed)**[1]	**Figueroa Colon & Woodbury (1996)**	**Quevado *et al.* (1990)**
Theophrastaceae		*Jacquinia umbellata*	
Acanthaceae		*Justica culebritae*	
Verbenaceae		*Lantana strigosa*	
Cactaceae		*Leptocereus quadricostatus*	*Leptocereus quadricostatus*
Ericaceae	*Lyonia truncata var. proctorii*	*Lyonia truncata var. proctorii*	
Malpighiaceae		*Malpighia setosa*	
Rubiaceae	*Mitracarpus maxwelliae*	*Mitracarpus maxwelliae*	*Mitracarpus maxwelliae*
Rubiaceae	*Mitracarpus polycladus*	*Mitracarpus polycladus*	*Mitracarpus polycladus*
Myrtaceae		*Myrciaria borinquena*	
Cactaceae		*Opuntia triacantha*	
Icacinaceae	*Ottoschulzia rhodoxylon*		*Ottoschulzia rhodoxylon*
Passifloraceae		*Passiflora bilobata*	
Passifloraceae		*Passiflora murucuja*	
Piperaceae		*Peperomia myrtifolia*	
Urticaceae		*Pilea richardii*	
Polygalaceae			*Polygala cowellii*
Polygalaceae		*Polygala hecatantha*	*Polygala hecatantha*
Portulacaceae		*Portulaca caulerpoides*	*Portulaca caulerpoides*
Arecaceae		*Pseudophoenix sargentii*	
Rubiaceae		*Randia portoricensis*	
Rhamnaceae			*Reynosia guama*
Boraginaceae			*Rochefortia cuneata*
Malvaceae		*Sida eggersii*	
Leguminosae	*Stahlia monosperma*	*Stahlia monosperma*	*Stahlia monosperma*
Bromeliaceae			*Tillandsia flexuosa*

Table 7.2 (continued).

Family	**U.S. Fish and Wildlife Service (Federally Listed)**[1]	**Figueroa Colon & Woodbury (1996)**	**Quevado *et al.* (1990)**
Bromeliaceae			*Tillandsia lineatispica*
Meliaceae	*Trichilia triacantha*	*Trichilia triacantha*	
Compositae	*Vernonia proctorii*	*Vernonia proctorii*	
Rutaceae	*Zanthoxylum thomasianum*	*Zanthoxylum thomasianum*	

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[1] Available over the Internet at http://endangered.fws.gov/

[2] *Cordia rupicola* is a candidate species for listing as an endangered species by the U.S. Fish and Wildlife Service; see http://endangered.fws.gov/

[3] Synonym of *Psychilis krugii* (Bello) Sauleda.

[4] Both *Myrtus bellonis* and *Eugenia bellonis* refer to the same species; the maerial is insufficient to determine the genus to which it belongs (Liogier 1994).

Cluster Analysis

Hierarchical clustering with complete linkage was used to group studied sites on the basis of similarity among the various metrics used to evaluate fragment conservation potential (see Legendre and Legendre, 1998 Chapter 8, for justification for the use of this method of clustering). Values used in the cluster analysis were transformed so as to scale to values between zero and one, in order to avoid imbalance in the weighting of the variables. Site history (as determined in Chapter 3) was compared with the clusters produced by this method. Analyses were carried out using Systat 9 (SPSS Inc., 1998).

Results

Species Richness/Species Density

The species richness of more than half of all fragments did not differ significantly from the value predicted by the species-area curve. Twenty-two fragments had residuals that were not significantly different from predicted values, seven had significantly more species than predicted and 10 had significantly fewer species than predicted (Table 7.3). Most Relict fragments (fragments that were more than 75% 'old growth'; see Chapter 3) had either significantly more species than predicted (six fragments) or did not differ from predicted species richness (11 fragments). Only three Relict fragments had fewer species than predicted (Table 7.3). Most Regrowth fragments (fragments that were more than 75% post-1936 regrowth; see Chapter 2) had either significantly fewer species than predicted (six fragments) or did not differ from predicted species richness (eight fragments). Only one Regrowth fragment had more species than predicted (Table 7.3).

Two Mixed fragments (fragments that were more than 25% but less than 75% post-1936 regrowth) did not differ significantly from predicted species richness, while one had significantly fewer species than predicted (Table 7.3). The pattern of distribution among the categories was not significantly different from what would be expected at random (Pearson's χ^2, 4 x 3 contingency table, $n = 39$, $p < 0.397$ for all categories; if the 'unknown' category was omitted, 3 x 3 contingency table, $n = 38$, $p < 0.257$). Species density matched the pattern displayed by the Standardized Residuals (Pearson correlation $r = 0.932$). Species densities ranged from 31 species/ha to 104 species ha^{-1} (Table 7.3). If the same calculation is performed using the area and species richness of Guánica Forest, a value of 227 species ha^{-1} is obtained (however, Guánica Forest does not fit the species-area curve calculated for the fragments; see Chapter 5). If the 'canonical' value of *z* is used (0.26; Preston, 1962) a species density of 89 is obtained for Guánica Forest, a value which is in line with the upper limit of values obtained for the fragments.

Representativity

Individual fragments supported between 7.1% and 85.7% of species in the reference lists compiled for each of the three main associations in Guánica Forest (Table 7.4). Individual fragments scored similarly against each list, reflecting the fact that the three associations overlap substantially in species composition (Table 7.1). Five fragments (Sites 1, 2, 4, 5, and 7) supported more than 75% of the species present in at

Table 7.3: Standardized residuals of the species-area curve (standardized residuals by χ^2 transformation) and "species density" (calculated from the species-area curve) of dry forest fragments in southwestern Puerto Rico. Symbols refer to fragments with significantly more species than expected (+), significantly fewer species than expected (-) or that did not differ significantly from expectations (o). Rank refers to the rank order of fragments in terms of species density.

Site	Area	Species Richness	History	Residual	Standardized Residual	Deviation	Species Density	Rank
7	33	149	Relict	41.0	15.6	+	95.6	3
21	1.2	104	Relict	33.1	15.4	+	101.6	2
36	0.04	69	Relict	22.9	11.4	+	103.8	1
15	3.7	112	Relict	30.2	11.1	+	94.9	4
30	0.2	77	Regrowth	20.5	7.4	+	94.5	5
18	1.5	93	Relict	20.0	5.5	+	88.3	6
5	101	148	Relict	23.6	4.5	+	82.4	8
10	5.1	101	Mixed	15.8	2.9	o	82.1	11
4	125	147	Relict	19.2	2.9	o	79.6	15
25	2.4	92	Mixed	14.5	2.7	o	82.3	9
27	0.4	74	Relict	12.3	2.4	o	83.1	10
8	7	103	Relict	14.3	2.3	o	80.4	12
14	6	101	Relict	14.0	2.3	o	80.4	13
31	0.11	63	Relict	10.6	2.1	o	83.4	7
34	0.07	57	Regrowth	7.5	1.1	o	79.9	14
26	1	76	Regrowth	6.7	0.6	o	76.0	16
11	2.6	82	Relict	3.8	0.2	o	72.6	17
12	3	81	[unknown]	1.3	0.0	o	70.5	18
28	0.8	68	Relict	0.6	0.0	o	70.0	19
1	1372	174	Relict	0.9	0.0	o	69.5	20
13	2	75	Relict	-0.7	0.0	o	68.7	21
22	1.2	68	Regrowth	-2.9	0.1	o	66.4	22
35	0.07	45	Regrowth	-4.5	0.4	o	63.1	24
23	1	64	Relict	-5.3	0.4	o	64.0	23

Table 7.3: (continued)

Site	Area	Species Richness	History	Residual	Standardized Residual	Deviation	Species Density	Rank
19	1.5	62	Regrowth	-11.0	1.7	o	58.9	25
16	3.3	68	Relict	-12.6	2.0	o	58.4	26
32	0.1	41	Regrowth	-10.8	2.2	o	54.9	27
39	0.01	28	Regrowth	-10.7	3.0	o	50.3	31
29	0.2	43	Regrowth	-13.5	3.2	o	52.8	30
37	0.02	29	Regrowth	-13.2	4.1	-	47.7	32
6	64	95	Relict	-22.4	4.3	-	56.0	28
33	0.09	35	Regrowth	-16.1	5.1	-	47.5	33
40	0.006	21	Regrowth	-15.3	6.4	-	40.2	36
2	770	125	Mixed	-35.9	8.0	-	53.7	29
17	6.3	58	Relict	-29.5	10.0	-	45.9	34
20	1.5	46	Regrowth	-27.0	10.0	-	43.7	35
38	0.01	17	Regrowth	-21.7	12.2	-	30.5	39
9	5.9	50	Relict	-36.8	15.6	-	39.9	37
24	1	31	Regrowth	-38.3	21.2	-	31.0	38

least one of the reference lists, and three sites (Sites 1, 5 and 7) had more than 75% of the species in the deciduous forest, semi-evergreen forest and scrub forest lists (Table 7.4). The smallest site that scored above 75% for any of the associations was Site 7 (33 ha).

A total of 19 sites supported > 50% of the reference list for at least one of the three associations. The smallest site to support > 50% of the reference list was Site 31 (0.11 ha) for the semi-evergreen forest association and the scrub forest association, and Site 36 (0.04) ha for the deciduous forest association (Table 7.4). Relict fragments supported 17.1-85.7% of the reference species while Mixed fragments supported 39.2-78.6% and Regrowth fragments supported 7.1-47.6% of the reference species. All fragments larger than 100 ha had > 75% representation. All fragments over 33 ha had > 50% representation.

Rare and Endangered Species

Twelve of the 53 rare or endangered species were present in at least one of the fragments (Table 7.5). The most widespread species, Leptocereus quadricostatus (Bello) Britton & Rose, was present in 18 fragments and the second most widespread, *Guaiacum sanctum*, was present in 11 fragments. Psychilis krugii (Bello) Sauleda was recorded from eight fragments, Jacquinia umbellata DC. from five fragments, Eugenia woodburyana Alain and Passiflora bilobata Juss. from four, Polygala cowellii (Britton) S.F. Blanke, Reynosia guama Urban and Trichilia triacantha Urban were present in two and Bourreria virgata (Sw.) G. Don, Cordia rupicola Urban and Randia portoricensis (Urban) Britton & Rose were present in only one fragment (Table 7.5). A total of 25 fragments supported at least one rare or endangered species. One fragment (Site 1) had nine rare or endangered species, two fragments (Sites 2 and 4) had five species, one

Table 7.4: Proportion of the species composition of the three main associations in Guánica Forest that are represented in sampled dry forest fragments, southwestern Puerto Rico. DeF = Deciduous Forest, SEv = Semi Evergreen Forest, ScF = Scrub Forest.

Site	Area	History	Percent DeF	Percent SEv	Percent ScF
1	1372	Relict	85.7	84.1	81.1
2	770	Mixed	78.6	73.0	78.4
4	125	Relict	67.1	79.4	71.6
5	101	Relict	84.3	84.1	78.4
6	64	Relict	52.9	57.1	52.7
7	33	Relict	75.7	79.4	78.4
8	7	Relict	50.0	55.6	48.6
9	5.9	Relict	31.4	30.2	36.5
10	5.1	Mixed	48.6	60.3	51.4
11	2.6	Relict	60.0	65.1	55.4
12	3	unknown	44.3	49.2	51.4
13	2	Relict	38.6	41.3	35.1
14	6	Relict	52.9	54.0	51.4
15	3.7	Relict	40.0	41.3	41.9
16	3.3	Relict	48.6	42.9	41.9
17	6.3	Relict	55.7	42.9	52.7
18	1.5	Relict	54.3	60.3	52.7
19	1.5	Regrowth	35.7	41.3	36.5
20	1.5	Regrowth	20.0	27.0	20.3
21	1.2	Relict	57.1	65.1	60.8
22	1.2	Relict	62.9	50.8	59.5
23	1	Relict	17.1	23.8	23.0
24	1	Regrowth	7.1	7.9	9.5
25	2.4	Mixed	42.9	54.0	39.2
26	1	Regrowth	37.1	41.3	36.5
27	0.4	Relict	38.6	39.7	35.1
28	0.8	Relict	50.0	46.0	51.4
29	0.2	Regrowth	25.7	31.7	21.6
30	0.2	Regrowth	42.9	47.6	37.8
31	0.11	Relict	52.9	54.0	51.4
32	0.1	Regrowth	25.7	33.3	31.1
33	0.09	Regrowth	12.9	19.0	14.8
34	0.07	Regrowth	30.0	38.1	32.4
35	0.07	Regrowth	27.1	33.3	24.3
36	0.04	Relict	50.0	46.0	48.7
37	0.02	Regrowth	22.9	22.2	23.0
38	0.01	Regrowth	15.7	15.9	14.9
39	0.01	Regrowth	18.6	17.5	18.9
40	0.006	Regrowth	14.3	17.5	16.2

Table 7.5: Distribution of rare and endangered species among studied dry forest fragments in southwestern Puerto Rico.

Species	Fragment Number																								
	1	2	4	5	6	7	8	10	11	12	13	14	15	16	17	18	19	21	22	25	26	27	28	31	36
Bourreria virgata	x																								
Cordia rupicola	x																								
Eugenia woodburyana			x				x													x		x			
Guaiacum sanctum	x	x		x		x		x				x		x	x	x	x		x						
Jacquinia umbellata		x	x					x				x				x									
Leptocereus quadricostatus		x	x	x	x	x	x	x	x		x		x	x	x		x	x			x	x		x	x
Passiflora bilobata	x	x				x				x															
Polygala cowellii	x								x																
Psychilis krugii	x	x		x		x								x					x			x	x		
Randia portoricensis	x																								
Reynosia guama	x		x																						
Trichilia triacantha	x		x																						

fragment (Sites 7) had four species, four fragments had three species, seven had two species, and 10 had one rare or endangered species (Table 7.5).

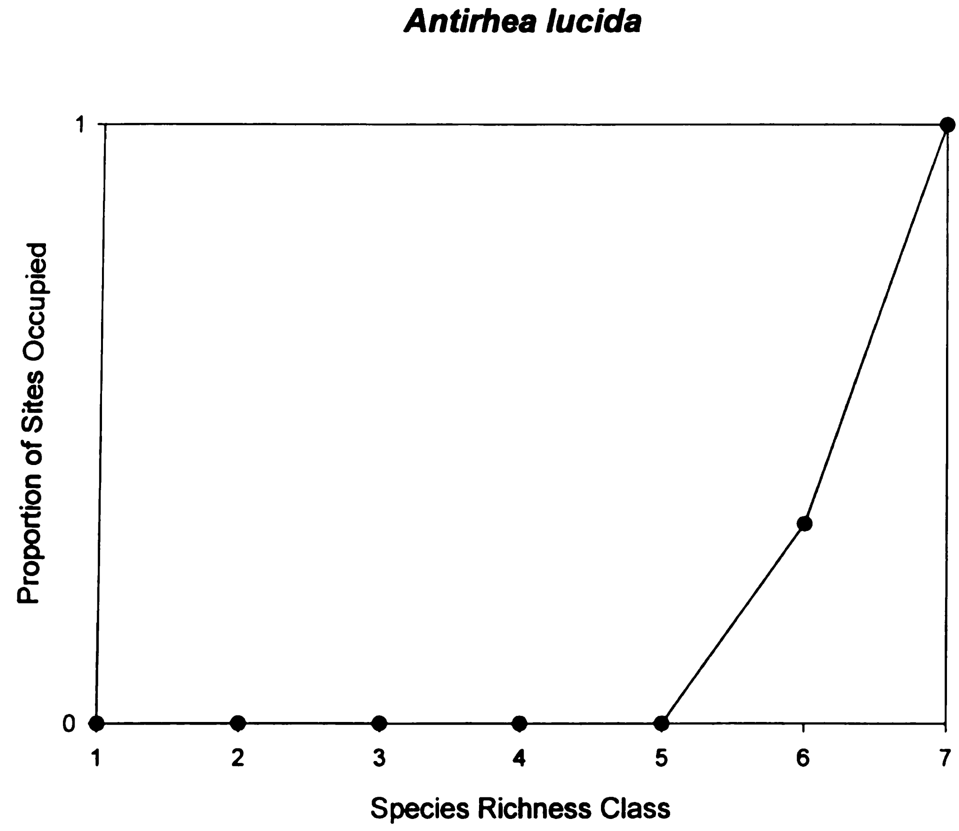
Indicator Species

A total of six species fit the criteria selected to identify potential indicator species (Figure 7.1a-f). These species were: *Antirhea lucida* (Sw.) Hook. f. (Rubiaceae), *Coccoloba diversifolia* Jacq. (Polygonaceae), *Cordia rickseckeri* Millsp. (Boraginaceae), *Guettarda krugii* Urb. (Rubiaceae), *Plumeria alba* L. (Apocynaceae) and *Savia sessiliflora* (Sw.) Willd. (Euphorbiaceae).

Three fragments supported all six Indicators (Sites 1, 5 and 7), two fragments supported five of them (Sites 4 and 15) and two fragments supported four of them (Table 7.6). Sixteen fragments supported none of the six Indicator species.

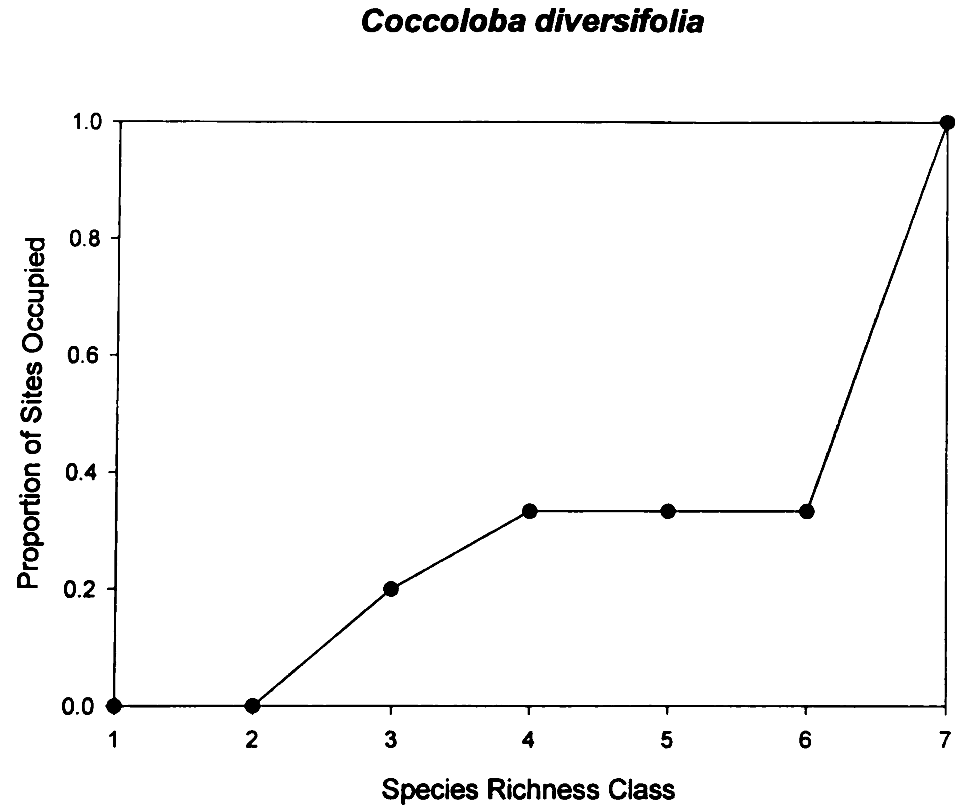
Cluster Analysis

The clustering algorithm yielded two groups of fragments based on measures of conservation potential, using a cut-off distance of 0.8 (Figure 7.2). One group consisted of 16 Relict fragments, three Mixed fragments and two Regrowth fragment and one fragment of unknown history. The second cluster consisted of six Relict fragments and twelve Regrowth fragments. The pairs of fragments that were most similar were Sites 8 and 14 and Sites 29 and 32. Fragments in cluster 2 were mainly located in the western and southern parts of the study area (Figure 7.3). Based on the constituent fragments, the first cluster appears to be fragments of higher conservation value, while the second cluster appears to be those of lower conservation value; fragments in cluster 1 averaged 2.7 Indicator species per site, while those in cluster 2 averaged 0.7 Indicators. No

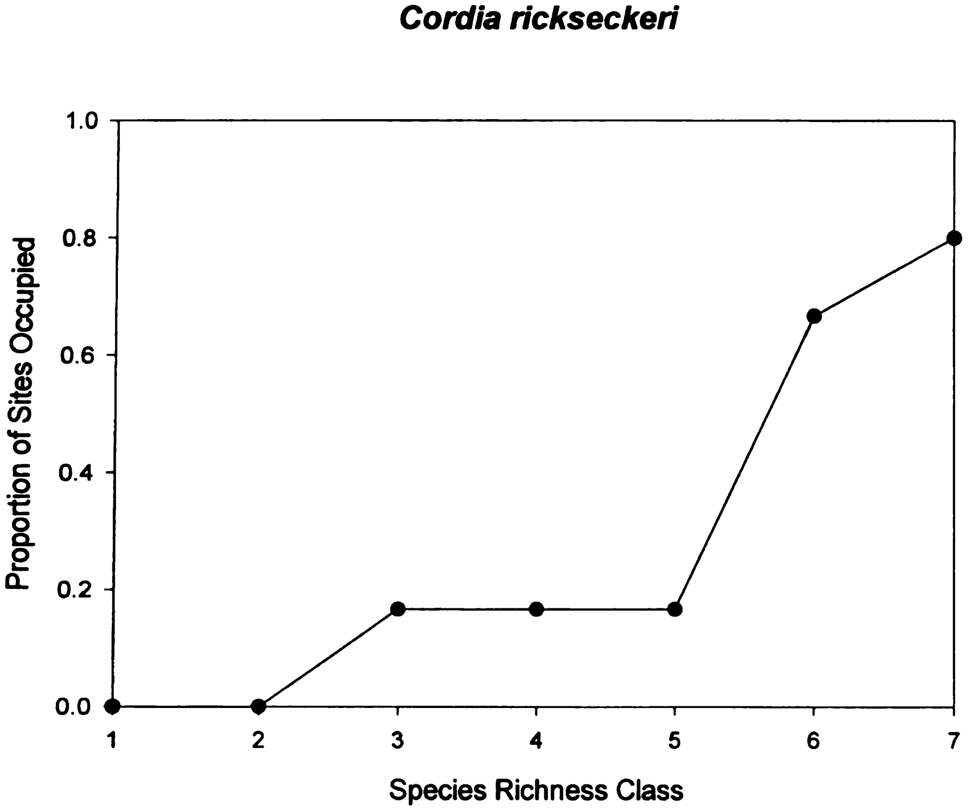


a. *Antirhea lucida*

Figure 7.1: Incidence functions (*sensu* Diamond 1975) for the six species present in dry forest fragments in southwestern Puerto Rico which met the criteria selected to identify indicators of sites with high conservation value. Species richness classes each consist of 5-6 fragments grouped on the basis of total plant species richness. Indicator species were defined as those which were present in less than 20% of the two most species-poor classes and were present in more than 80% of the fragments in the most species-rich class.

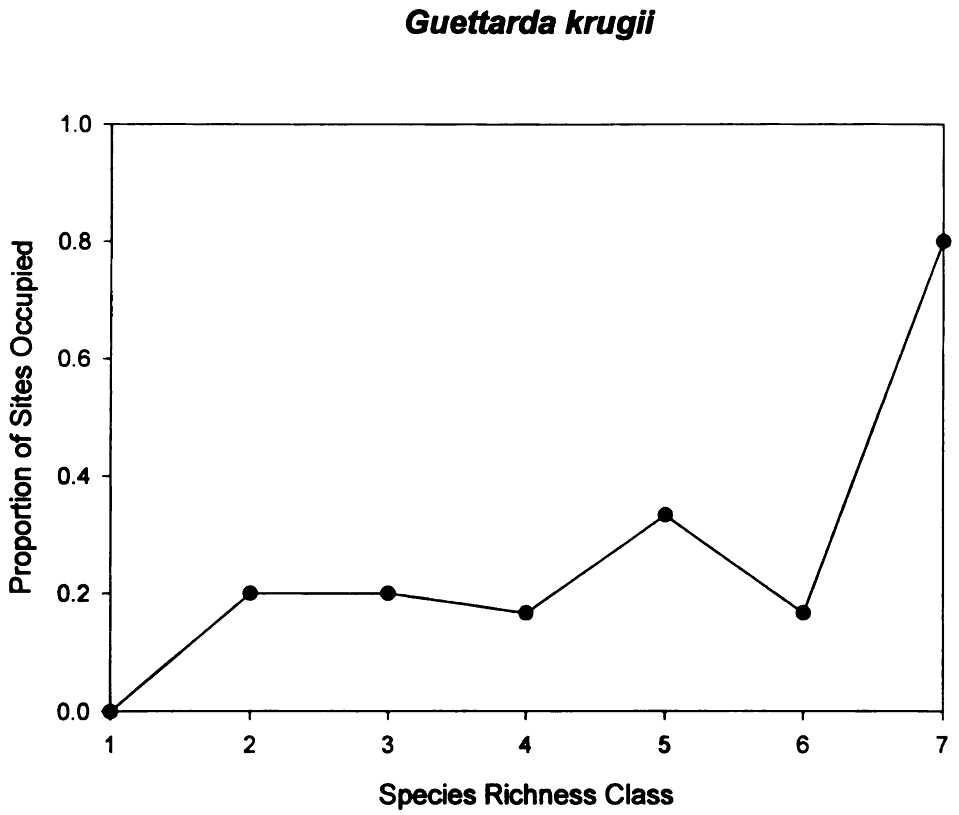


b. *Coccoloba diversifolia*

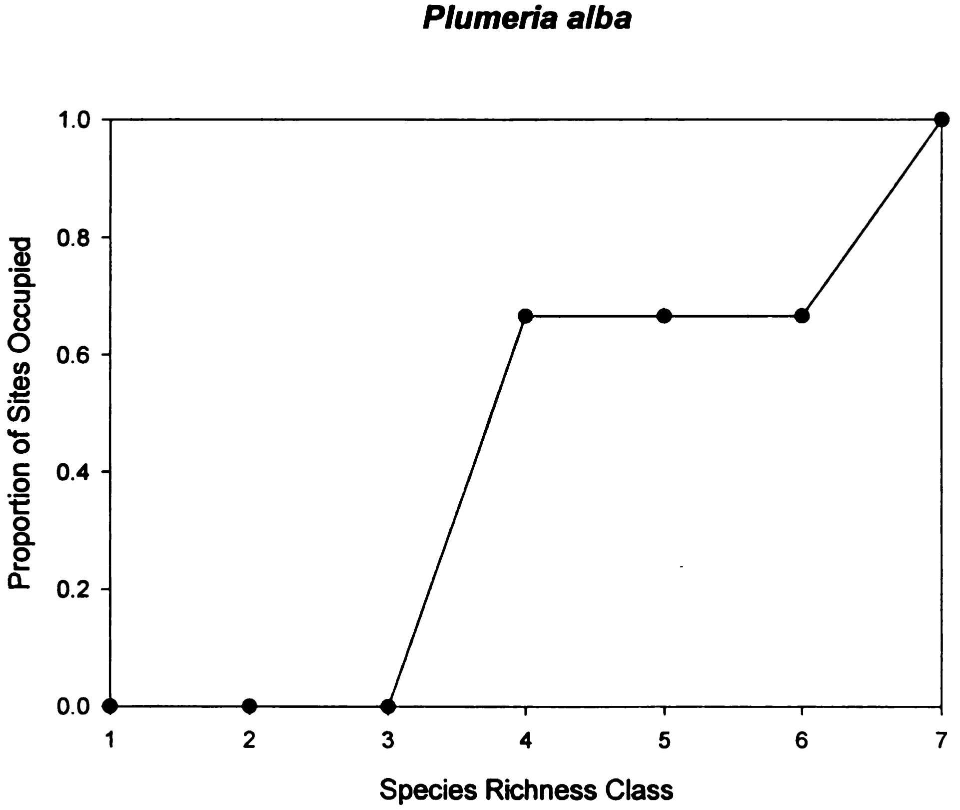


c. *Cordia rickseckeri*

Figure 7.1 (continued).

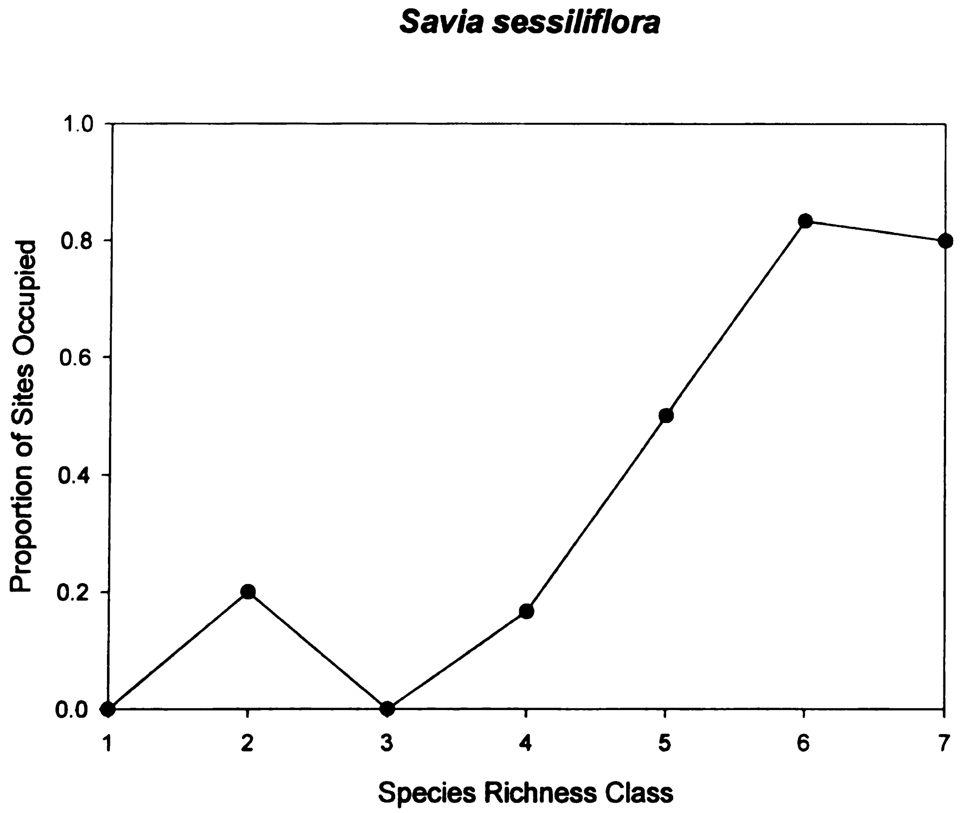


d. *Guettarda krugii*



e. *Plumeria alba*

Figure 7.1 (continued).



f. *Savia sessiliflora*

Figure 7.1 (continued).

Table 7.6: The number of plant species among the six proposed Indicators of fragments of high conservation potential which were present in studied dry forest fragments in southwestern Puerto Rico.

Site	Area	History	Species Richness	Number of Indicators
1	1372	Relict	174	6
2	770	Mixed	125	4
3	45	Regrowth	--	0
4	125	Relict	147	5
5	101	Relict	148	6
6	64	Relict	95	3
7	33	Relict	149	6
8	7	Relict	103	4
9	5.9	Relict	50	1
10	5.1	Mixed	101	0
11	2.6	Relict	82	0
12	3	unknown	81	2
13	2	Relict	75	0
14	6	Relict	101	3
15	3.7	Relict	112	5
16	3.3	Relict	68	2
17	6.3	Relict	58	1
18	1.5	Relict	93	2
19	1.5	Regrowth	62	1
20	1.5	Regrowth	46	0
21	1.2	Relict	104	2
22	1.2	Relict	68	2
23	1	Relict	64	0
24	1	Regrowth	31	0
25	2.4	Mixed	92	3
26	1	Regrowth	76	0
27	0.4	Relict	74	3
28	0.8	Relict	68	3
29	0.2	Regrowth	43	2
30	0.2	Regrowth	77	0
31	0.11	Relict	63	0
32	0.1	Regrowth	41	0
33	0.09	Regrowth	35	0
34	0.07	Regrowth	57	1
35	0.07	Regrowth	45	0
36	0.04	Relict	69	2
37	0.02	Regrowth	29	0
38	0.01	Regrowth	17	0
39	0.01	Regrowth	28	0
40	0.006	Regrowth	21	0

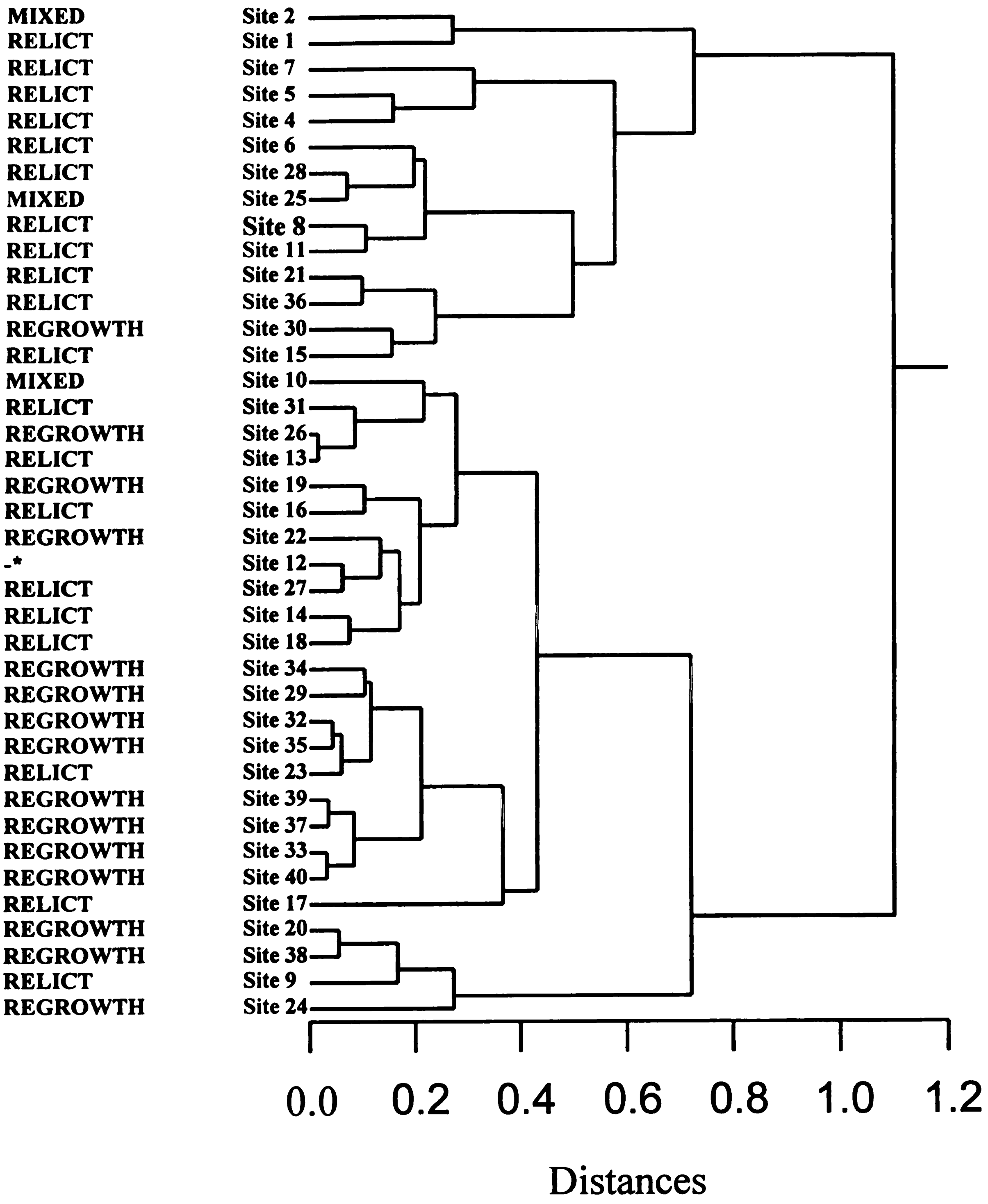


Figure 7.2: Hierarchical clustering dendrograms of Puerto Rican dry forest fragments based on scores of their Conservation Potential.

fragments in cluster 2 had more than three Indicator species, and only one (Site 6) had more than two of them.

Discussion

Species Richness/Species Density

There were no surprises among the fragments whose species richness differed significantly from predicted values. The fragments with the largest negative standardized residuals (Sites 9 and 24) were also outliers in the fragment community classification (Chapter 4). Site 9 was very species-poor. The community was dominated by two woody species, *Erithalis fruticosa* and *Coccoloba microstachya*; 66.3% of all individuals sampled in this fragment belonged to these two species. This site was located on a windswept peninsula and probably had the most extreme environment of all the studied fragments. It was also the most isolated – it was part of the only cluster of fragments that was more than 1000 m from other clusters of forest fragments (Chapter 3). Site 24 supported a community that did not gain membership in any other cluster on the basis of species composition (Chapter 4); it was also more mesic than any of the other studied fragments (personal observation).

Most of the fragments with large positive residuals had shrunk significantly in the 1936-1993 period. It seems reasonable to assume that these fragments are 'oversaturated' (*sensu* Diamond 1972): they currently have more species than they would support at equilibrium. It is likely that enough time has not elapsed for them to have reached equilibrium. However, in the case of Site 21 (the fragment with the second-largest standardized residual) it seems more reasonable to invoke the intermediate disturbance hypothesis (Connell 1978). This fragment had an open canopy and was grazed by cattle (personal observation) – it seemed a prime candidate for weed invasion, but much of the original species complement appears to have still been present (it supports 51-61% of the species on the reference lists; Table 7.4)

Measures of species per unit area are qualitatively similar to the standardized residuals of the species-area curve. Whittaker *et al.* (2001) argues against using measures of species density that are estimated statistically since they tend to incorporate 'other information' about the site, and in doing so may mask the real relationship between per-plot species richness and fragment species richness (see Chapter 5). It is precisely this property of the estimated value of *c* that makes it a useful measure of fragment conservation value. If species richness (or some metric derived from species richness) is to be used as a measure of fragment conservation potential, it should reflect the factors that make the site richer in species than might be predicted on the basis of area. Habitat heterogeneity is a factor of this type.

Representativity

This is perhaps the most intuitively appealing of the measures of fragment conservation value. It would seem reasonable that a fragment with a species composition resembling that of the reference community would be functionally similar to that community. However, macroecology theory suggests otherwise. Common species are likely to be widespread, while rare species are likely to have more restricted distributions (Gaston *et al.* 1997) although the pattern of incidence of Guánica Forest species in the fragments is somewhat more complicated than that (see Chapter 6). Nonetheless, there is a general pattern where some species (that are 'common' inasmuch as that they were included in the relatively small sample that was used to compile this reference list) are present in most of the fragments regardless of the overall 'quality' of the fragments. These 'ubiquitous' species are, in fact, likely to be present in almost all fragments, which may be a function (at least in part) of their ability to utilize matrix (non-forest) habitat. As was shown in Chapter 6, the species that are most abundant in Guánica Forest are not those that are the most widespread among fragments – in fact, these dominant species are absent from many Regrowth fragments. See Chapter 6 for a more detailed analysis of these types of species patterns.

Large fragments show high representation. Five of the six largest fragments that were inventoried had > 75% representation across all three of the reference lists. The only large fragment with < 75% representation (Site 6) was partly grazed in the 1930s (R. Carlo, personal communication). Several very small fragments had high representation, consistent with the predictions of the "more of the same' model (Thomas 2004). Two fragments smaller than 0.5 ha supported > 50% of the reference lists. It was immediately apparent in the field that these fragments were high-quality remnants of dry forest. The fact that fragments this small could support such a large number of the reference species illustrates the resilience of dry forests, especially since the smaller of them (Site 36, 0.04 ha) was already mostly isolated in 1936. Unfortunately, this fragment was destroyed by fire in the 1998 dry season (S. Van Bloem, personal communication). Thus illustrates a fundamental weakness of small fragments – their elevated susceptibility to disturbance (Janzen 1983, 1986b, Viana and Tabanez 1996, Viana *et al.* 1997, Cochrane and Laurance 2002).

The idea that small fragments can support a substantial proportion of the native community agrees with findings by (Pither and Kellman 2002) who found that 25 small fragments (ranging in size from 325 m^2 to 3625 m^2 were able to support 106 of the 160 tree species present in large fragments of gallery forest in Belize, and by (Thomas 2004) who found that 85% of the species in five focal genera present in a 50-ha plot at Pasoh Forest Reserve, Malaysia, were present in 12 1-ha forest fragments which had been isolated for about 25 years.

Rare and Endangered Species

The presence of a species of concern in any fragment makes it valuable. On the other hand, the presence of endangered species does not always indicate the presence of high quality habitat (Gilfedder and Kirkpatrick 1998). In this instance, the presence of rare and endangered species was not the best tool for identifying fragments of high conservation value. The two most widespread species on the list, *Leptocereus quadricostatus* and *Guaiacum sanctum* L. were present in fragments that were not otherwise seen as having high conservation value. *Leptocereus quadricostatus* is a narrowly endemic species restricted to the dry forest zone of southwestern Puerto Rico. Any species endemic to so heavily degraded a habitat should be seen as being at risk. Concern for this species was also expressed regarding disease (Quevedo *et al.* 1990). Similarly, *G. sanctum* is a rare species that has been over-harvested historically. However, it does not appear to be as rare as Quevedo *et al.* (1990) thought it to be. Both of these species are fleshy-fruited and appear to be vertebrate-dispersed (see Ricart Morales, 1999, for details of the dispersal of *G. officinale*, an ecologically similar species with similar fruit; Liogier 1988). In addition, *L. quadricostatus* appears to be able to colonize regrowth and survive in heavily disturbed areas; it was present, for example, in Site 26, a Regrowth fragment in the middle of a cattle pasture. As a spiny cactus, it is likely to be resistant to browsing by cattle.

Most of the species on the list of rare and endangered species were not present in the sampled forest fragments, although the possibility exists that they were misidentified or overlooked. The fragments that supported the largest number of rare and endangered species were large and species-rich. As a measure of fragment conservation potential, rare and endangered species added several fragments that would not have been otherwise considered valuable, but the information is difficult to interpret.

Indicator Species

Seven of the eight largest fragments were among the fragments that had four or more of the six proposed indicators. The sole exception was Site 6, with only three indicator species which was also the only large fragment with > 75% representation. Unlike the other assessment systems, the system of indicator species did not confer a high value to small fragments; Site 36 had only two of the six indicators and Site 31 had none. The system was developed using species with high fidelities for the most species-rich sites. Given the relationship between species richness and area, these tend to be large fragments. The rationale for using several species as indicators was to minimize the effects of the presence or absence of a single species: metapopulation theory predicts that species will be absent from some portion of their suitable habitat. Similarly, a single species may be a relic of a different community that had been incorporated into a

Regrowth fragment as it expands. The use of several species amounts to a measurement that is somewhat closer to a 'community' measure.

All six of the species selected are distinctive and readily identifiable in the field. This should make them easy to use in field surveys. Another advantage of highly detectable species as indicators is that the probability of them turning up in a survey if they are present should be high. Even if species lists are incomplete, easily detectable species are likely to turn up, while more cryptic species might not be recorded. This feature of the proposed indicators was not selected *a priori*, but nonetheless is likely to increase the utility of these species as indicators.

Cluster Analysis

The clustering algorithm produced two well-separated clusters. The 'high conservation value' cluster consisted mostly of Relict or Mixed fragments. Most of the Relict fragments in the 'lower value' cluster were either highly disturbed (*e.g.*, Site 11) or were purely 'coastal' fragments. Despite the fact that these fragments are likely to have a low species density (as a consequence of their being rocky with very little soil), they are valuable in that they represent a distinct community which, by virtue of its location on the seas shore, is likely to represent especially favored sites for the development of resorts and holiday homes. These fragments also supported littoral species which were not present in other sites.

The location of the two groups of fragments (Figure 7.3) indicates that there is some degree of spatial separation between high and low conservation value clusters. In addition to the coastal fragments, fragments at the drier end of the spectrum may also be more likely to end up in the lower-value cluster. It is possible that the two clusters represent wetter and drier groups of fragments, rather than higher- and lower-value fragments, but this interpretation is not supported by differences in history between the two fragments clusters. It is also possible that the difference may relate to recovery after disturbance. The recovery of dry forest after disturbance may be slower in drier sites than in wetter sites. It is also possible that development pressures were greater in drier sites, resulting in fewer Relict sites at the dry end of the spectrum.

The results of the cluster analysis agree broadly with fragment history and the system of proposed Indicator species in terms of the definition of more and less valuable fragments. Unfortunately, the classes are somewhat broad – while it might be desirable to protect all fragments in the 'higher value' cluster, it is probably impracticable to do so.

There are two philosophical positions from which to approach the search for sites of high conservation value. One can either approach the question mechanistically, and in doing so try to use the correlates of 'valuable' sites to attempt to predict other sites which would be likely to be of high conservation value, or one could approach it from a purely practical point of view and try to identify sites that need protection on a case-by-case basis. The weakness of the former case lies in the fact that ecology remains a complex and often poorly understood science – identification of correlates of high value sites does not guarantee that the underlying causal factors will be discovered. On the other hand, simply carrying out inventories to search for valuable sites or to find species of concern is likely to be inefficient and require a large number of specially trained staff. In addition, if little is known about the conditions that allow a site to support a 'valuable' species assemblage, then one has no idea how to ensure that the site remains 'valuable'. While the idea of designating Indicator species is a first attempt to streamline the process of surveying fragments, it still needs to be tested and refined.

Summary

1) Twenty-two fragments did not differ significantly from the species richness predicted by the species-area curve, seven fragments had significantly more species and 10 had significantly fewer species than predicted.
2) Of the seven fragments with significantly more species than predicted, six were Relict and one was Regrowth.
3) Of 10 fragments with significantly fewer species than predicted, three were Relict, six were Regrowth and one was Mixed. The pattern of distribution of histories among the groups did not differ significantly from random.
4) Fragments supported between 7.1% and 85.7% of the reference species.
5) Five fragments supported more than 75% of the species on at least one of the three reference lists; three of them supported more than 75% of the species on all three reference lists.
6) Nineteen fragments supported more than 50% of the species on at least one of the reference lists; the smallest fragment with more than 50% of the species on at least one of the reference lists was 0.04 ha.
7) Twelve of 53 rare or endangered species were present in at least one of the fragments; the most widespread of these species were *Leptocereus quadricostatus* and *Guaiacum sanctum*.

8) Twenty-five fragments supported at least one of the rare or endangered species; only two Federally listed endangered species (*Eugenia woodburyana* and *Trichilia triacantha*) was present in any of the fragments (in four and two fragments respectively). With nine of these species, Site 1 was overwhelmingly the most important fragment in terms of rare and endangered species

9) Six species were designated potential indicators of sites of high conservation value on the basis of their meeting the criteria designated; these species were *Antirhea lucida*, *Coccoloba diversifolia*, *Cordia rickseckeri*, *Guettarda krugii*, *Plumeria alba* and *Savia sessiliflora*.

10) Two well separated clusters were identified on the basis of the criteria outlined to determine conservation value of these fragments.

CHAPTER 8: CONCLUSIONS AND RECOMMENDATIONS

Conclusions

Puerto Rican dry forest fragments (including the large fragment, Guánica Forest) represent the last remnants on the island of Puerto Rico of a vanishing biome. The abandonment of agriculture in Puerto Rico and the concomitant return of forest cover provide an opportunity to manage the landscape for the preservation of the native biota and the survival of this community type. It is not only important to attempt to preserve the species that are present; it is also important to attempt to preserve their genetic diversity.

Relict forest fragments are able to harbor a representative assemblage of plant species (up to as much as 86% of the reference species; Chapter 7), but many Regrowth fragments do not – *Gymnanthes lucida*, *Croton humilis* and *C. discolor* were only present in 6.3% of all Regrowth fragments (Chapter 6). Instead, most Regrowth fragments are dominated by *Leucaena leucocephala*. While forest cover has been able to recover without intervention (Chapter 3) this forest often lacks the community dominants, even as much as 50 years after abandonment (Molina Colón 1998). In light of this, it may be necessary to re-introduce these species into Regrowth forest.

It is impossible to attempt to restore Puerto Rican dry forest to its pristine condition, given the uncertainty as to what would constitute 'pristine' vegetation. One can attempt to re-create a hypothetical 'climax community' much like Gleason and Cook (1926) did, but there is no guarantee that restoration would yield a forest that resembled their '*Bucida* series'. While Murphy and Lugo (1986b) suggested that the short, multi-stemmed nature of the forest was a consequence of historic cutting, Dunphy *et al.* (2000) found that the condition was natural. Nonetheless, this does not constitute proof that the original vegetation was short and multi-stemmed historically. It was suggested that the original vegetation might be unrecoverable because erosion may have stripped much of the topsoil of the original community after the trees were cut, resulting in the present short-stature, multi-stemmed forest (F. Wadsworth, personal communication). It is also possible that the draining of Laguna Guánica altered the rainfall regime, resulting in a more xeric community than existed initially. On the other hand, Van Bloem *et al.* (in press) have shown that the multi-stemmed condition may be caused by wind storms, a fact which suggests that the forest may have always been short-statured and multi-stemmed.

Nepstad and colleagues (Nepstad *et al.* 1994, Jipp *et al.* 1998, Moreira *et al.* 2000) have shown that deep soil moisture plays an important role in the water relations of dry forest trees in Pará in the Brazilian Amazon. Trees that are able to access deep soil moisture continue to transpire much later into the dry season than do pasture grasses. While some trees appear to have access to soil moisture in Puerto Rican dry forest because they remain green and appear to be transpiring throughout the dry season (*e.g.*, *Guaiacum officinale*; Gleason and Cook, 1926, Castilleja, 1991), no one has measured the role of this resource. In that light, it is impossible to attempt to estimate the change that may have occurred with the loss of the original forests, and whether trees in second growth are able to access deep soil moisture at all.

What we are left with then is a need to manage an already highly impacted community whose ecology is still not well enough known. However, the reality of the situation is that some sort of pro-active management is essential. Development will continue along Puerto Rico's south coast. As development proceeds, forest will be lost, even as more pasture is abandoned and reverts to forest. Molina Colón (1998) has shown that even fairly old Regrowth does not begin to resemble relict forest (in terms of species composition), although, as has been shown in Chapter 4, some Relict forest can be degraded to something that resembles Regrowth without ever actually being cleared. The preservation of Relict forest fragments must be seen as a priority by agencies responsible for granting permits for development. Chapter 7 presents some tools that can be used to identify fragments that are likely to be of high conservation value. These tools must be used, tested and refined, and their predictive power relative to animal species must be tested.

The most effective tools for conservation are also the most expensive. The purchase of land for the purpose of conservation and the purchase of conservation easements are valuable tools for conservation, but they are expensive. Without public support, it is also expensive to police the borders of reserves (see Allen 2001). Education is another valuable tool – based on my interactions with members of the public, they were all aware of the value of *bosque seco* (dry forest), but they were aware of it in the singular sense – the Bosque Seco (*i.e.*, Guánica Forest). Many people did not seem to connect the idea of dry forest with the forest fragments amongst which they live. Half the task has been achieved, but more needs to be done to create an appreciation of the dry forest fragments outside of Guánica Forest.

Priority areas for conservation outside of protected areas must be identified. The expansion of the Laguna Cartagena National Wildlife Reserve to include land in the

Sierra Bermeja is a valuable start, but the whole Sierra Bermeja must be formally identified as a priority area. Similarly, a good spatial perspective is essential. As demonstrated in Chapter 3, the strips of forest across the Lajas Valley should also be high priority areas. The southern strip, just north of the town of La Parguera, is likely to be at especially high risk. For the most part these are not Relict forest, although there are many Relict patches embedded in a larger matrix of Regrowth; it is likely that these forests would not be identified as being of high conservation value using the tools in Chapter 7. Their value lies in their spatial context. If these forests are preserved and expanded, it may be possible to create and maintain gene flow between Guánica Forest and the Sierra Bermeja.

Several patches of forest to the north of Guánica Forest may constitute another high-priority corridor. The Commonwealth Forests of Susua and Maricao lie in the southwestern portion of the Cordillera Central, and are the nearest large protected areas to Guánica Forest. The southern slopes of these forests support vegetation that shares many species in common with Guánica Forest – although they are in the moist forest life zone, the steep south-facing slopes are fairly dry. It is important to maintain gene flow between the plants on these slopes and their conspecifics in the dry forest zone. Thus, the corridor north of Guánica Forest is likely to be another priority area.

Forest sites adjacent to Guánica Forest are also likely to be priority areas. There is privately owned forestland between Guánica Forest and the protected area that was studied as Site 4. Maintaining this band of forest between the two protected areas is important to the maintenance of the biological integrity of Site 4. It is also important to maintain a buffer around Guánica Forest where still possible – already the community of

La Luna has grown to the very edge of the forest, and the forest also abuts the town of Guánica. Maintaining a forested buffer along the northern and eastern edges of the park is critical.

The largest of the studied fragments was Site 1. This fragment, to the northeast of Guánica Forest, supports *Trichilia triacantha*, a federally listed endangered species. Most of the fragment is privately owned, and is adjacent to housing developments in several areas. Protection of this biologically rich fragment is important, as are the fragments to the east of it in the Tallaboa area.

East of Tallaboa and west of Ponce is a large patch of dry forest that was not considered under this study due to the absence of defined fragments. However, cursory examination has shown that large parts of this area support mixed-species forest and not *Leucaena leucocephala*-dominated regrowth. This status is predictable since the area was forested in the 1936 aerial photographs, even though it appeared to be heavily disturbed. Several endangered species and a species that is a candidate for listing have also been recorded in a portion of this block of forest. This area consists of at least 1000 ha of dry forest; if much of this forest is actually mixed-species forest, it may have a critical role to play in the conservation of Puerto Rican dry forest. It is critically in need of further study.

Further Questions

As questions are answered, further ones arise. Some of the areas which seem to need to be addressed are:

1) Examine the role of species in accelerating and encouraging succession. Young secondary forests tend to be dominated by *Leucaena leucocephala* and are species-poor, but not all Regrowth forest is of this sort. Several distinct hypotheses are available regarding successional pathways, and these need to be tested
    a. Shade: evergreen species cast deeper shade, which is likely to encourage succession.
    b. Focal trees: fleshy-fruited species are attractive to frugivores, which are likely to be seed dispersers. Higher levels of seed input are likely to accelerate succession. Additionally, species which are not themselves fleshy-fruited but which are parasitized by mistletoes (mostly members of the Loranthaceae and Viscaceae) provide food to frugivores. *Pisonia albida* is one of the most consistently and heavily infested trees in the study area (personal observation).
    c. Water/Nutrients: strips of forest have been observed to develop along seasonal streams in the study area. Although these areas are Regrowth, they are support species-rich forest which clustered with Relict fragments on the basis of species composition.

    These hypotheses need to be tested experimentally.
2) Deeper understanding of the role of *Leucaena leucocephala* in the process of succession; does it inhibit succession through competition, does it provide an inhospitable environment for the establishment of seedlings because it is dry-

season deciduous, or does it simply fail to attract seed dispersers because it is not fleshy fruited?

3) Based on the identification of 'old' patches (areas within existing fragments which have been forested continuously since the 1930s), actively search out rare species.
4) Use spatially explicit models to predict the movement of species – seeds, seed dispersers and pollinators – across the landscape, and use these to improve connectivity through restoration and enrichment planting.
5) Use population genetic tools to examine the levels of genetic diversity within fragments and among fragments to determine how well the existing genetic diversity is captured in protected areas.
6) Focus on a larger suite of species to address the question of how different species and groups of species have responded to long-term habitat fragmentation.

APPENDICES

APPENDIX 1

FRAGMENT-SPECIES OCCURRENCE MATRIX

Table A1: Species-site occurrence matrix for plants in Puerto Rican dry forest fragments.

Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Acanthaceae	*Oplonia microphylla*	x																			
	Oplonia spinosa	x																			
	Ruellia tuberosa				x		x	x	x		x	x	x	x						x	x
	Siphonoglossa sessilis	x	x		x		x	x	x		x	x	x	x	x	x			x	x	x
	Stenandrium tuberosum	x																			
Agavaceae	*Agave* sp.	x										x				x			x		
Amaranthaceae	*Achyranthes aspera*				x				x	x										x	x
	Celosia nitida	x			x	x	x	x	x		x	x		x		x				x	
	Iresine angustifolia	x							x												
Anacardiaceae	*Comocladia dodonaea*	x	x		x	x	x	x	x		x	x	x	x	x	x	x	x	x		
Apocynaceae	*Plumeria rubra*	x	x		x	x		x	x				x		x	x	x		x		
	Prestonia agglutinata	x			x									x	x						
	Rauvolfia nitida	x									x										
	Rauvolfia viridis	x				x	x	x	x												
Arecaceae	*Roystonea* sp.																				
	Thrinax morrisis	x															x				
Asteraceae	P081																				x
	Wedelia lanceolata	x	x			x		x	x						x		x	x			
Bignoniaceae	*Crescentia cujete*																			x	
	Distictis lactiflora	x	x		x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x
	Macfaydena unguis-cati	x	x		x	x	x	x	x		x	x	x	x	x	x			x	x	x
	P108																				
	Tabebuia heterophylla	x	x			x		x		x			x			x	x	x		x	
	Tecoma stans					x					x										
Bombacaceae	*Ceiba pentandra*				x																
Boraginaceae	*Bourreria domingensis*					x															
	Bourreria succulenta	x	x		x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x
	Bourreria virgata	x																			
	Cordia alliodora																				

Table A1: continued.

Family	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Acanthaceae	*Oplonia microphylla*																				
	Oplonia spinosa																				
	Ruellia tuberosa	x					x				x				x	x	x				
	Siphonoglossa sessilis			x	x	x	x	x	x	x	x				x	x		x	x	x	
	Stenandrium tuberosum																				
Agavaceae	*Agave* sp.					x			x												
Amaranthaceae	*Achyranthes aspera*	x					x								x	x					
	Celosia nitida	x				x	x		x		x		x		x						
	Iresine angustifolia																				
Anacardiaceae	*Comocladia dodonaea*	x	x			x	x	x	x	x	x	x	x		x		x	x	x		x
Apocynaceae	*Plumeria rubra*	x	x			x		x	x								x				
	Prestonia agglutinata																				
	Rauvolfia nitida																				
	Rauvolfia viridis	x				x		x	x	x	x			x		x				x	
Arecaceae	*Roystonea* sp.				x																
	Thrinax morrisis		x			x															
Asteraceae	P081																				
	Wedelia lanceolata	x	x					x								x					
Bignoniaceae	*Crescentia cujete*															x					
	Distictis lactiflora	x	x	x		x	x	x	x	x	x		x		x	x	x	x	x	x	x
	Macfaydena unguis-cati	x		x		x	x	x		x	x	x	x		x	x					
	P108					x															
	Tabebuia heterophylla	x	x								x	x					x				
	Tecoma stans				x		x														
Bombacaceae	*Ceiba pentandra*																				
Boraginaceae	*Bourreria domingensis*																				
	Bourreria succulenta	x	x	x		x	x	x	x	x	x	x			x	x	x	x	x	x	x
	Bourreria virgata																				
	Cordia alliodora				x																

Table A1: continued.

Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Boraginaceae	*Cordia borinquensis*																				
	Cordia bullata		x		x		x	x	x		x	x	x	x		x				x	
	Cordia collococca					x															
	*Cordia ricksecke*ri	x			x	x	x	x	x							x					
	Cordia rupicola	x																			
	Heliotropium angustiflium	x	x		x	x	x	x	x		x	x	x	x		x			x	x	x
	Rochfortia acanthophora	x	x		x	x		x	x		x	x		x		x		x	x	x	x
	Tournefortia microphylla		x		x		x	x		x	x	x	x	x	x	x			x		
	Tournefortia scabra	x			x																
Bromeliaceae	*Bromelia pinguin*	x			x	x		x	x				x			x				x	
	P003	x	x		x	x		x								x	x		x		
	P004	x	x		x	x		x								x			x		
	P005							x													
	Tillandsia recurvata	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Tillandsia usneoides				x																
Burseraceae	*Bursera simaruba*	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x		x		
Cactaceae	*Hylocereus trigonus*	x			x		x	x	x		x		x						x		x
	Leptocereus quadricostatus		x		x	x	x	x	x		x	x		x		x	x	x		x	
	Melocactus intortis		x					x	x									x			
	Opuntia repens		x		x		x	x	x		x	x		x		x	x			x	x
	Opuntia sp.1		x					x		x	x	x								x	
	Opuntia sp.2					x								x							
	Pilosocereus royenii	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Canella winterana	x	x		x	x	x	x		x	x				x			x	x		
Capparidaceae	*Capparis baducca*				x		x														
	Capparis cynophallophora or *C. indica*	x	x		x	x	x	x	x		x	x	x	x	x	x	x	x	x		x
	Capparis flexuosa	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x
	Capparis hastata	x	x		x	x	x	x	x		x			x	x	x		x	x	x	x

Table A1: continued.

Family	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Boraginaceae	*Cordia borinquensis*							x													
	Cordia bullata	x		x		x	x		x		x		x		x	x	x	x	x	x	x
	Cordia collococca			x																	
	Cordia rickseckeri	x									x				x		x				
	Cordia rupicola																				
	Heliotropium angustiflium	x					x		x		x			x	x	x	x	x		x	x
	Rochfortia acanthophora	x	x			x					x	x					x		x	x	
	Tournefortia microphylla	x	x				x		x		x	x	x		x	x	x	x	x	x	x
	Tournefortia scabra																				
Bromeliaceae	*Bromelia pinguin*			x		x				x											
	P003							x													
	P004																				
	P005					x		x													
	Tillandsia recurvata	x		x		x	x	x	x	x	x	x	x		x	x	x	x	x	x	
	Tillandsia usneoides																				
Burseraceae	*Bursera simaruba*	x	x	x		x	x	x	x	x	x	x	x			x		x			
Cactaceae	*Hylocereus trigonus*					x		x													
	Leptocereus quadricostatus	x					x	x				x					x				
	Melocactus intortis							x													
	Opuntia repens	x		x		x	x	x		x	x	x	x		x	x	x				
	Opuntia sp.1	x				x		x								x	x				
	Opuntia sp.2	x																			
	Pilosocereus royenii	x		x		x	x	x	x	x	x	x	x		x	x	x	x			x
	Canella winterana											x									
Capparidaceae	*Capparis baducca*			x		x	x				x										
	Capparis cynophallophora or *C. indica*	x	x		x	x	x	x	x	x	x	x	x		x		x				
	Capparis flexuosa	x	x			x	x	x	x	x	x	x	x		x	x					
	Capparis hastata	x				x	x	x	x	x	x	x			x	x		x		x	

Table A1: continued.

Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Caricaceae	*Carica papaya*				x																
Celastraceae	*Cassine xylocarpa*	x	x			x		x												x	
	Gyminda latifolia					x															
	Maytenus sp.	x																			
	Schaefferia frutescens	x			x	x	x		x		x	x	x			x		x	x		
	T028		x																		
Clusiaceae	*Clusia minor* or *C. rosea*	x			x	x			x							x					
Combretaceae	*Bucida buceras*	x	x		x	x	x	x	x		x	x	x		x	x		x	x	x	
	Conocarpus erectus									x							x				
Commelinaceae	*Commelina erecta*	x	x		x		x	x	x	x	x	x	x			x	x		x	x	x
Convolvulaceae	*Ipomoea arenaria*	x																			
	Ipomoea pes-caprae		x																		
	Jacquemontia spp.	x	x		x	x	x	x	x		x		x	x	x				x	x	
	P104				x	x	x	x		x	x	x				x					
Crassulaceae	*Bryophyllum pinnatum*						x		x												
	Bryophyllum sp.1													x							
	Bryophyllum sp.2							x													
Cycadaceae	*Zamia pumila*	x		x	x										x				x		
Cyperaceae	C024														x						
	C025																x				
	P041	x						x							x		x		x	x	
	P042																x				
	P043																x				
Elaeocarpaceae	*Muntingia calabura*														x						
Erythroxylaceae	*Erythroxylum areolatum*		x					x		x	x			x	x	x	x				x
	Erythroxylum brevipes	x		x				x	x		x	x	x		x	x			x		
	Erythroxylum rotundifolium	x	x		x					x							x	x			
	Erythroxylum urbanii	x																			
Euphorbiaceae	*Acalypha portoricensis*	x	x		x			x	x												

Table A1: continued.

Family	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Caricaceae	*Carica papaya*																				
Celastraceae	*Cassine xylocarpa*							x				x				x					
	Gyminda latifolia		x																		
	Maytenus sp.																				
	Schaefferia frutescens	x	x						x		x					x	x				
	T028																				
Clusiaceae	*Clusia minor* or *C. rosea*					x		x		x											
Combretaceae	*Bucida buceras*	x	x			x	x		x	x	x	x			x		x				
	Conocarpus erectus																				
Commelinaceae	*Commelina erecta*	x		x		x	x	x	x	x	x	x	x		x		x				x
Convolvulaceae	*Ipomoea arenaria*	x																			
	Ipomoea pes-caprae																				
	Jacquemontia spp.	x	x	x		x		x	x		x	x	x				x				
	P104	x															x				
Crassulaceae	*Bryophyllum pinnatum*			x		x	x	x													
	Bryophyllum sp.1																				
	Bryophyllum sp.2																				
Cycadaceae	*Zamia pumila*																				
Cyperaceae	C024																				
	C025																				
	P041																				
	P042																				
	P043																				
Elaeocarpaceae	*Muntingia calabura*				x																
Erythroxylaceae	*Erythroxylum areolatum*					x		x								x					
	Erythroxylum brevipes			x		x		x		x											
	Erythroxylum rotundifolium																				
	Erythroxylum urbanii																				
Euphorbiaceae	*Acalypha portoricensis*					x															

Table A1: continued.

Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Euphorbiaceae	*Adelia rincinella*											x		x		x			x		x
	Argythamnia candicans or *A. stahlii*	x	x		x	x	x	x			x	x	x	x	x	x		x	x		
	Argythamnia fasiculata	x	x		x	x	x	x			x	x	x	x	x	x			x		
	Bernardia dichotoma	x	x		x	x		x			x		x		x	x			x		
	Chamaesyce articulata	x								x											
	Chamaesyce spp.											x					x				
	Croton betulinus	x	x		x	x		x							x				x		
	Croton discolor	x	x		x	x	x	x		x		x		x		x	x	x			
	Croton humilis	x	x		x	x	x	x		x	x		x		x		x	x	x		
	Croton rigidus	x	x		x	x		x			x	x	x	x	x				x		
	Dalechampia scandens	x	x		x	x	x	x	x		x		x		x	x			x		x
	Euphorbia cyathophora				x	x	x	x	x		x		x		x						
	Euphorbia lactea		x											x							
	Euphorbia petiolaris				x											x					
	Fluggea acidoton											x		x		x			x		
	Gymnanthes lucida	x	x		x	x		x					x		x	x		x	x		
	Jatropha gossypifolia				x		x	x						x	x	x		x			
	Jatropha hernandiifolia	x			x	x		x							x	x					
	P009								x												
	Pedilanthus tithymaloides ssp. *angustifolia*	x						x					x			x					
	Phyllanthus epiphyllanthus	x				x															
	Savia sessiliflora	x			x	x	x	x	x				x		x	x					
	Tragia volubilis	x	x		x		x	x			x	x	x			x				x	x
Flacourtiaceae	*Samyda dodecandra*	x	x		x	x		x	x				x		x	x					
	Xylosoma buxifolia	x				x															
Krameriaceae	*Krameria ixina*					x				x							x	x			
Lauraceae	*Cassytha filiformis*																x				
Leguminosae	*Abrus precatorius*								x				x								x

Table A1: continued.

Family	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Euphorbiaceae	*Adelia rincinella*										x	x									
	Argythamnia candicans or *A. stahlii*	x	x				x		x	x	x	x	x		x	x		x	x	x	x
	Argythamnia fasiculata	x				x		x				x									
	Bernardia dichotoma							x	x			x									
	Chamaesyce articulata																				
	Chamaesyce spp.						x				x					x	x				
	Croton betulinus	x	x				x	x	x		x		x				x	x		x	
	Croton discolor	x	x						x								x				
	Croton humilis		x						x			x									
	Croton rigidus	x		x	x	x		x				x					x				
	Dalechampia scandens	x		x		x		x							x		x		x		x
	Euphorbia lactea	x							x												
	Euphorbia petiolaris																				
	Fluggea acidoton																				
	Gymnanthes lucida	x	x						x			x					x				
	Jatropha gossypifolia	x		x	x				x	x	x		x				x				
	Jatropha hernandiifolia																				
	P009							x													
	Pedilanthus tithymaloides ssp. *angustifolia*																				
	Phyllanthus epiphyllanthus																				
	Savia sessiliflora					x		x	x	x											
	Tragia volubilis	x		x			x				x		x			x	x		x		x
Flacourtiaceae	*Samyda dodecandra*	x		x		x		x		x		x					x				
	Xylosoma buxifolia																				
Krameriaceae	*Krameria ixina*																				
Lauraceae	*Cassytha filiformis*																				
Leguminosae	*Abrus precatorius*			x		x		x													

Table A1: continued.

Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Leguminosae	*Acacia farnesiana*		x			x								x	x						
	Acacia retusa	x	x		x	x	x	x	x		x	x	x		x	x			x		
	Caesalpinia bonduc		x							x											
	Centrosema sp.		x		x		x	x		x	x	x				x	x			x	x
	Coursetia caribaea	x			x	x	x	x	x		x	x	x	x	x	x			x	x	x
	Crotalaria lotofolia	x	x		x	x		x											x		
	Delonix regia					x															
	Desmanthus virgatus	x													x						
	Desmodium sp.																				
	Galactia spp.	x	x		x	x	x	x	x		x	x	x	x			x	x	x	x	x
	Haematoxylum campechianum										x				x						
	Hymaenea courbaril																				
	Leucaena leucocephala	x	x		x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x
	P001				x																
	P002																				
	P006																x				
	P015				x	x		x			x				x	x					
	P016				x						x	x									
	P022					x															
	P040									x											
	P048																				
	P078	x																	x		
	P096	x																			
	P113																				
	Pictetia aculeata	x	x		x	x		x	x			x	x		x	x		x	x	x	x
	Piscidia carthagenensis						x		x										x	x	x
	Pithecellobium unguis-cati	x	x		x	x		x	x		x	x		x	x	x		x	x	x	
	Poitea florida	x	x			x		x							x				x		
	Prosopis pallida		x	x				x			x	x		x	x	x	x	x			x

Table A1: continued.

Family	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Leguminosae	*Acacia farnesiana*	x			x	x															
	Acacia retusa			x		x	x		x	x	x	x									
	Caesalpinia bonduc																				
	Centrosema sp.	x		x	x			x			x				x	x	x	x			x
	Coursetia caribaea	x	x			x	x	x	x	x		x	x		x	x	x			x	x
	Crotalaria lotofolia																				
	Delonix regia																				
	Desmanthus virgatus																				
	Desmodium sp.			x	x																
	Galactia spp.	x	x	x	x		x	x	x		x		x		x		x				
	Haematoxylum campechianum																				
	Hymaenea courbaril			x																	
	Leucaena leucocephala	x	x	x	x	x	x	x	x	x	x	x	x			x	x	x	x	x	x
	P001				x																
	P002				x																
	P006																				
	P015																				
	P016	x			x			x									x				
	P022																				
	P040																				
	P048												x								
	P078			x																	
	P096																				
	P113				x																
	Pictetia aculeata		x			x										x					
	Piscidia carthagenensis	x				x	x	x		x	x				x		x				
	Pithecellobium unguis-cati	x	x	x	x	x	x	x	x		x	x	x		x	x	x	x	x		
	Poitea florida												x								
	Prosopis pallida	x					x				x		x		x	x				x	

Table A1: continued.

Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Leguminosae	*Senna polyphylla*	x				x				x				x			x				
	Senna sp.1		x																		
	Tamarindus indica	x				x				x				x							x
	Zapoteca portoricensis	x																			
Liliaceae	*Aloe vera*													x						x	
	Sanseveria trifasciata	x				x													x		
Malpighiaceae	*Bunchosia glandulosa*	x			x	x								x		x					
	Heteropterys purpurea	x	x		x	x	x	x	x		x	x	x		x	x		x	x	x	
	Stigmaphyllon emarginatum	x	x		x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x
Malvaceae	*Bastardia viscosa*		x		x		x	x				x		x	x	x					
	Gossypium sp.											x		x			x	x			
	Hibiscus clypeatus				x	x		x													
	Hibiscus phoencius	x	x		x	x	x	x	x		x	x	x	x	x	x			x	x	x
	Malvastrum americanum											x			x						
	P018	x	x		x		x	x		x	x		x			x		x		x	
	P019				x																
	P023											x									
	P036		x																		
	P046				x		x	x	x		x	x	x	x		x					
	P055							x			x										
	P061																				
	Sh044				x		x	x	x		x					x					
	Sh048				x	x			x		x			x							
	Sh049	x			x		x	x	x		x		x								
	Sh050							x													
Meliaceae	*Swietenia mahogani*					x															
	Trichilia hirta	x			x	x	x	x	x		x	x				x			x		
	Trichilia triacantha	x			x																
Moraceae	*Ficus citrifolia*	x			x												x				

Table A1: continued.

Family	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Leguminosae	*Senna polyphylla*		x																		
	Senna sp.1																				
	Tamarindus indica					x												x			
	Zapoteca portoricensis																				
Liliaceae	*Aloe vera*																				
	Sanseveria trifasciata														x						
Malpighiaceae	*Bunchosia glandulosa*		x				x				x										
	Heteropterys purpurea	x	x			x	x	x	x	x		x	x		x	x	x				
	Stigmaphyllon emarginatum	x	x	x	x	x	x	x	x		x	x	x			x	x	x	x	x	x
Malvaceae	*Bastardia viscosa*	x		x			x						x	x		x	x				
	Gossypium sp.	x					x														
	Hibiscus clypeatus																				
	Hibiscus phoencius	x		x		x	x	x	x			x			x	x	x				
	Malvastrum americanum						x														
	P018	x													x						
	P019																				
	P023																				
	P036																				
	P046	x		x		x	x	x	x		x	x									
	P055							x													
	P061				x																
	Sh044	x				x		x	x						x						
	Sh048																				
	Sh049	x																			
	Sh050																				
Meliaceae	*Swietenia mahogani*		x																		
	Trichilia hirta			x	x	x	x	x		x	x				x		x				
	Trichilia triacantha																				
Moraceae	*Ficus citrifolia*																				

Table A1: continued.

Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Moraceae	*Maclura tinctoria*	x						x													
Myrtaceae	*Eugenia axillaris*	x			x	x		x						x	x				x		
	Eugenia biflora						x														
	Eugenia foetida	x	x		x	x		x				x		x	x		x	x	x		
	Eugenia lingustrina	x			x	x	x	x	x		x		x	x		x			x		
	Eugenia monticola	x			x	x							x								
	Eugenia procera	x	x												x						
	Eugenia rhombea	x	x		x	x	x	x	x		x			x	x	x	x				
	Eugenia woodburyana				x				x												
	Eugenia xerophytica	x	x			x				x									x		
	Myrciaria floribunda								x												
	Psidium amplexicaule																				
	T029		x																		
	T030		x																		
	T031					x															
Nyctaginaceae	*Guapira fragrans*	x							x												
	Neea buxifolia								x										x		
	Pisonia aculeata	x												x							
	Pisonia albida	x	x		x	x	x	x			x		x	x	x	x	x	x	x	x	
	Pisonia subcordata															x					
Oleaceae	*Chionanthus holdridgei*	x																			
	Forestiera segregata		x		x	x				x		x	x				x				
	Jasminum fluminense	x			x	x	x	x			x	x		x	x	x			x	x	
	Ximenia americana		x											x				x			
	Mesadenus polyanthus				x			x					x								
	Oeceoclades maculata	x			x			x													
	P031																				
	P032	x																			
	P033	x																			

Table A1: continued.

Family	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Moraceae	*Maclura tinctoria*																				
Myrtaceae	*Eugenia axillaris*		x			x				x											
	Eugenia biflora																				
	Eugenia foetida		x	x								x					x				
	Eugenia lingustrina	x						x				x									
	Eugenia monticola			x		x															
	Eugenia procera																				
	Eugenia rhombea	x	x				x		x			x				x					
	Eugenia woodburyana					x		x													
	Eugenia xerophytica		x																		
	Myrciaria floribunda														x						
	Psidium amplexicaule							x													
	T029																				
	T030																				
	T031																				
Nyctaginaceae	*Guapira fragrans*					x		x		x	x										
	Neea buxifolia																				
	Pisonia aculeata		x																		
	Pisonia albida	x	x	x					x		x		x				x	x	x	x	x
	Pisonia subcordata																				
Oleaceae	*Chionanthus holdridgei*																				
	Forestiera segregata	x							x								x				
	Jasminum fluminense			x	x	x	x		x		x	x									
	Ximenia americana																				
Orchidaceae	*Mesadenus polyanthus*								x												
	Oeceoclades maculata																				
	P031							x													
	P032																				
	P033																				

Table A1: continued.

Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Orchidaceae	*Psychilis krugii*	x	x			x		x									x				
	Vanilla spp.	x	x		x	x		x								x					
	Passiflora andenica							x													
	Passiflora bilobata	x	x					x					x								
	Passiflora suberosa	x	x			x	x	x	x	x	x				x	x	x	x	x		x
Phytolaccaceae	*Trichostigma octandrum*	x				x															
Piperaceae	*Peperomia questeliana*								x							x					
	Peperomia robustior	x																			
Plumbaginaceae	*Plumbago scandens*											x									
Poaceae	*Grass* sp.1	x	x		x	x	x	x	x		x	x	x	x	x	x			x	x	x
	Grass sp.2												x	x	x						
	Grass sp.3	x	x		x	x	x	x		x	x	x		x	x		x		x	x	
	Grass sp.8		x		x	x				x				x							
	Lasiascis divaricata	x	x		x	x		x					x		x	x		x	x		
Polygalaceae	*Polygala cowellii*				x							x									
Polygonaceae	*Coccoloba diversifolia*	x	x		x	x	x	x							x	x	x		x	x	
	Coccoloba krugii	x	x			x	x	x		x						x		x			
	Coccoloba microstachya	x	x		x	x		x	x	x			x		x	x	x	x	x		
	Coccoloba swartzii	x																			
	Coccoloba uvifera									x							x				
Polypodiaceae	*Chelianthes microphylla*							x	x			x	x			x					
	H033								x												
Rhamnaceae	*Colubrina arborescens*	x	x		x	x	x	x	x	x	x		x	x	x		x	x		x	
	Colubrina elliptica		x		x		x	x	x			x				x	x			x	x
	Crossopetalum rhacoma	x	x		x	x	x	x		x	x	x		x	x			x	x		
	Gouania polygama	x	x		x	x	x	x	x		x	x	x		x	x			x		
	Krugiodendron ferreum	x	x		x	x	x	x	x		x		x	x	x	x			x		
	Reynosia guama	x			x																

Table A1: continued.

Family	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Orchidaceae	*Psychilis krugii*		x					x	x												
	Vanilla spp.		x						x								x				
	Passiflora andenica																				
	Passiflora bilobata																				
	Passiflora suberosa	x				x		x										x		x	x
Phytolaccaceae	*Trichostigma octandrum*																				
Piperaceae	*Peperomia questeliana*					x		x													
	Peperomia robustior								x												
Plumbaginaceae	*Plumbago scandens*						x														
Poaceae	*Grass* sp.1	x	x	x	x	x	x	x		x	x	x	x		x	x	x	x		x	
	Grass sp.2						x				x						x				
	Grass sp.3	x					x			x	x	x	x		x	x	x	x		x	
	Grass sp.8	x	x	x					x												
	Lasiascis divaricata																				
Polygalaceae	*Polygala cowellii*																				
Polygonaceae	*Coccoloba diversifolia*		x																		
	Coccoloba krugii		x																		
	Coccoloba microstachya	x	x					x	x			x					x	x		x	
	Coccoloba swartzii																				
	Coccoloba uvifera																				
Polypodiaceae	*Chelianthes microphylla*								x												
	H033																				
Rhamnaceae	*Colubrina arborescens*		x			x															
	Colubrina elliptica	x					x		x			x									
	Crossopetalum rhacoma	x	x						x								x				
	Gouania polygama			x		x	x			x											
	Krugiodendron ferreum	x	x			x	x		x			x	x		x						
	Reynosia guama																				

Table A1: continued.

Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Rhamnaceae	*Reynosia uncinata*	x	x		x	x		x				x				x	x			x	
	Ziziphus reticulata	x	x			x	x			x	x						x			x	
	Antirhea acutata	x	x		x	x	x	x	x			x			x	x	x	x			
Rubiaceae	*Antirhea lucida*	x	x		x	x		x	x							x					
	Catesbaea parviflora	x																			
	Chiococca alba or *C. parviflora*				x	x					x										
	Erithalis fruticosa	x	x			x				x							x	x			
	Ernodea littoralis									x							x				
	Exostema caribaeum	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
	Guettarda elliptica	x	x		x	x	x	x	x		x	x	x		x	x		x	x		
	Guettarda krugii	x	x			x		x		x								x			
	Guettarda odorata	x			x				x												
	Machaonia portoricensis																		x		
	P039							x													
	P079	x																			
	P089					x															
	P090	x																			
	Psychotria sp.	x																			
	Randia aculeata	x	x			x	x	x	x	x	x	x	x	x	x	x		x	x	x	x
	Randia portoricensis	x																			
	Rondelita inermis	x				x		x			x	x									
	Spermacoce confusa																				x
	Strumpfia maritima																x				
Rutaceae	*Amyris balsamifera*															x					
	Amyris elemifera	x	x		x	x	x	x	x		x		x		x	x			x		
	Zanthoxylum flavum	x				x	x	x			x			x			x	x			
	Zanthoxylum martinicensis	x			x															x	
	Zanthoxylum monophyllum	x			x		x		x		x		x			x					

Table A1: continued.

Family	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Rhamnaceae	*Reynosia uncinata*		x								x	x									
	Ziziphus reticulata					x					x					x		x			
	Antirhea acutata	x	x					x	x								x				
Rubiaceae	*Antirhea lucida*																				
	Catesbaea parviflora																				
	Chiococca alba or *C. parviflora*					x															
	Erithalis fruticosa		x								x										
	Ernodea littoralis																				
	Exostema caribaeum	x	x			x	x		x		x	x	x				x			x	x
	Guettarda elliptica	x	x						x			x									
	Guettarda krugii					x		x	x												
	Guettarda odorata	x					x					x									
	Machaonia portoricensis																				
	P039																				
	P079																				
	P089																				
	P090																				
	Psychotria sp.																				
	Randia aculeata	x		x		x				x	x				x	x	x	x		x	
	Randia portoricensis																				
	Rondelita inermis											x									
	Spermacoce confusa										x										
	Strumpfia maritima																				
Rutaceae	*Amyris balsamifera*																				
	Amyris elemifera	x	x			x		x	x		x	x	x		x		x				
	Zanthoxylum flavum		x								x	x					x				
	Zanthoxylum martinicensis			x																	
	Zanthoxylum monophyllum			x		x										x					

Table A1: continued.

Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Rutaceae	*Zanthoxylum spinifex*					x															
Sapindaceae	*Hypelate trifoliata*	x	x					x							x						
	Meliococcus bijugatis				x	x					x										x
	Serjania polyphylla	x			x	x		x	x		x	x	x	x	x	x			x		
	Thouinia striata	x	x		x	x	x	x	x		x	x	x		x	x		x	x	x	
Sapotaceae	*Chrysophyllum oliviforme*	x																			
	P020																				
	Sideroxylon obovatum	x	x			x		x		x				x			x		x		
	Sideroxylon salicifolium	x			x	x													x		
Scrophulariaceae	*Capraria biflora*																				
Smilacaceae	*Smilax coriacea*	x				x									x						
Solanaceae	P050															x					
	Solanum americanum		x		x	x	x	x	x	x	x	x		x	x	x	x			x	x
	Solanum persicifolium	x	x		x	x	x	x	x		x	x	x	x	x	x					
Sterculiaceae	*Ayenia insulaecola*		x				x	x				x	x		x			x		x	x
	Guazuma ulmifolia										x										
	Helicteres jamaicensis	x	x		x	x		x			x		x		x	x		x	x		
	Melochia tomentosa	x	x		x	x		x	x			x					x		x		x
Theophrastaceae	*Jacquinia armillaris*		x							x							x	x			
	Jacquinia berteroi	x	x			x										x					
	Jacquinia umbellata		x		x						x				x				x		
Tiliaceae	*Corchorus hirsutus*	x					x					x					x			x	
Turneraceae	*Turnera diffusa*	x	x			x		x		x					x		x				
Ulmaceae	*Celtis trinervia*	x			x		x	x				x				x					
Verbenaceae	*Citharexylum fruticosa*	x			x	x		x	x		x		x		x	x		x			
	Lantana camara	x			x		x	x	x		x									x	
	Lantana involucrata	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Stachytarpheta strigosa	x	x												x						
Visacaceae	*Phoradendron* spp.		x		x			x													

Table A1: continued.

Family	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Rutaceae	*Zanthoxylum spinifex*																				
Sapindaceae	*Hypelate trifoliata*		x																		
	Meliococcus bijugatis		x		x	x															
	Serjania polyphylla	x		x	x	x	x	x		x	x	x			x	x					
	Thouinia striata	x	x			x	x	x	x		x	x			x	x	x	x			
Sapotaceae	*Chrysophyllum oliviforme*						x														
	P020										x										
	Sideroxylon obovatum	x	x			x				x	x	x									
	Sideroxylon salicifolium					x															
Scrophulariaceae	*Capraria biflora*						x														
Smilacaceae	*Smilax coriacea*																				
Solanaceae	P050																				
	Solanum americanum			x		x	x			x	x		x		x	x					
	Solanum persicifolium	x		x		x	x				x				x						
Sterculiaceae	*Ayenia insulaecola*	x		x		x	x		x		x	x	x				x	x			x
	Guazuma ulmifolia			x		x				x											
	Helicteres jamaicensis											x									
	Melochia tomentosa	x	x				x					x			x						
Theophrastaceae	*Jacquinia armillaris*																				
	Jacquinia berteroi		x																		
	Jacquinia umbellata																				
Tiliaceae	*Corchorus hirsutus*	x		x																	
Turneraceae	*Turnera diffusa*	x	x				x											x			
Ulmaceae	*Celtis trinervia*						x				x										
Verbenaceae	*Citharexylum fruticosa*			x	x	x	x		x	x											
	Lantana camara				x	x		x							x						
	Lantana involucrata	x		x		x	x	x			x	x	x		x		x	x	x	x	x
	Stachytarpheta strigosa			x																	
Visacaceae	*Phoradendron* spp.	x									x		x					x	x	x	

Table A1: continued.

Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Vitaceae	*Cissus trifoliata*	x	x		x	x	x	x	x		x	x	x	x		x	x	x	x		
Zygophyllaceae	*Guaiacum officinalis*	x	x		x	x	x	x	x		x	x		x	x	x	x	x		x	
	Guaiacum sanctum	x	x			x		x			x				x		x	x	x	x	
Unknown	H036																				
	H037														x		x				
	H039							x													
	H040																				
	H042															x					
	H052																				
	P010				x																
	P011								x												
	P012		x				x			x					x	x					
	P014				x																
	P024														x						
	P025	x																			
	P026		x	x						x	x										
	P035		x	x							x										
	P038															x					
	P044							x													
	P100					x															
	P101				x			x				x	x			x			x	x	x
	P109	x	x			x		x											x		
	P110				x		x	x	x		x	x		x		x					
	P114																x				
	P117					x													x		
	P118					x															
	P119							x													
	P120	x																			
	P121	x				x	x	x		x	x								x		

Table A1: continued.

Family	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Vitaceae	*Cissus trifoliata*	x	x			x	x		x		x	x			x		x				
Zygophyllaceae	*Guaiacum officinalis*	x	x			x	x			x	x	x	x		x		x				
	Guaiacum sanctum		x																		
Unknown	H036		x																		
	H037	x									x										
	H039													x							
	H040													x							
	H042																				
	H052										x										
	P010																				
	P011					x															
	P012	x																			
	P014																				
	P024																				
	P025																				
	P026																				
	P035					x															
	P038																				
	P044																				
	P100																				
	P101		x												x		x				
	P109	x	x						x			x			x		x			x	
	P110	x		x	x	x	x			x	x	x					x				
	P114																				
	P117																				
	P118																				
	P119																				
	P120																				
	P121		x																		

Table A1: continued.

Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Unknown	P045																				
	P047							x													
	P049	x			x	x		x	x		x	x	x	x	x	x			x	x	
	P051																				
	P052																				
	P053				x																
	P054								x												
	P056																				
	P060																				
	P062																				
	P063																				
	P064						x														
	P065																x				
	P066																				
	P067					x		x	x		x		x		x				x		
	P068																				
	P069																				
	P070												x								
	P071												x								
	P072												x								
	P073																				
	P074																				
	P076																				
	P077	x																			
	P080					x	x		x												
	P082								x												x
	P083								x									x			
	P084	x																			

Table A1: continued.

Family	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Unknown	P045	x																			
	P047																				
	P049	x		x		x	x		x		x	x	x		x	x	x				
	P051						x														
	P052						x														
	P053																				
	P054							x	x												
	P056														x						
	P060				x																
	P062			x																	
	P063			x																	
	P064																				
	P065																				
	P066			x																	
	P067			x				x	x		x						x			x	
	P068			x																	
	P069			x																	
	P070																				
	P071																				
	P072																				
	P073															x					
	P074	x																			
	P076					x				x											
	P077																				
	P080	x																			
	P082			x		x	x	x		x					x						
	P083							x													
	P084																				

Table A1: continued.

Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Unknown	P085					x															
	P086					x															
	P087																		x		
	P088	x																			
	P093													x							
	P094							x													
	P095						x														
	P097				x																
	P098					x															
	Sh013					x															
	Sh020								x												
	Sh021							x													
	Sh022								x												
	Sh045														x						
	Sh047														x						
	Sh048				x		x		x		x					x				x	x
	Sh051														x						
	Sh053														x						
	T001	x					x								x				x		
	T006																				
	T008																				
	T009													x							
	T009						x														
	T013					x															
	T015		x																		
	T033		x																		
	T041																				

Table A1: continued.

Family	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Unknown	P085																				
	P086																				
	P087																				
	P088																				
	P093																				
	P094																				
	P095																				
	P097																				
	P098																				
	Sh013																				
	Sh020																				
	Sh021																				
	Sh022																				
	Sh045																				
	Sh047																				
	Sh048			x		x														x	
	Sh051	x					x		x		x				x	x					
	Sh053																				
	T001																				
	T006							x													
	T008										x										
	T009																				
	T009																				
	T013																				
	T015																				
	T033																				
	T041						x														

APPENDIX 2

DOMINANCE-DIVERSITY CURVES FOR PUERTO RICAN DRY FOREST FRAGMENTS

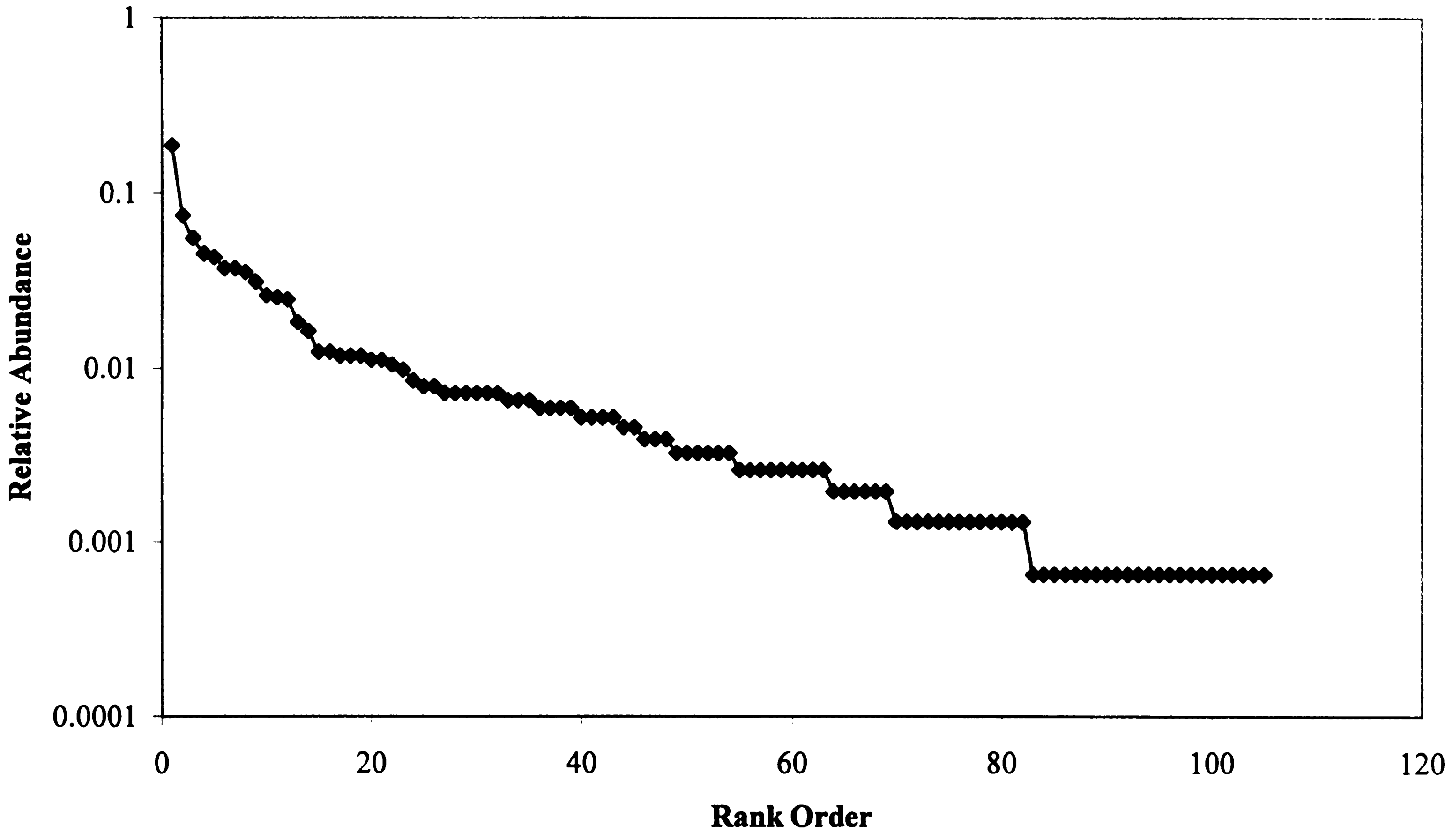


Figure B2.1: Dominance-diversity curve of Site 1, southwestern Puerto Rico

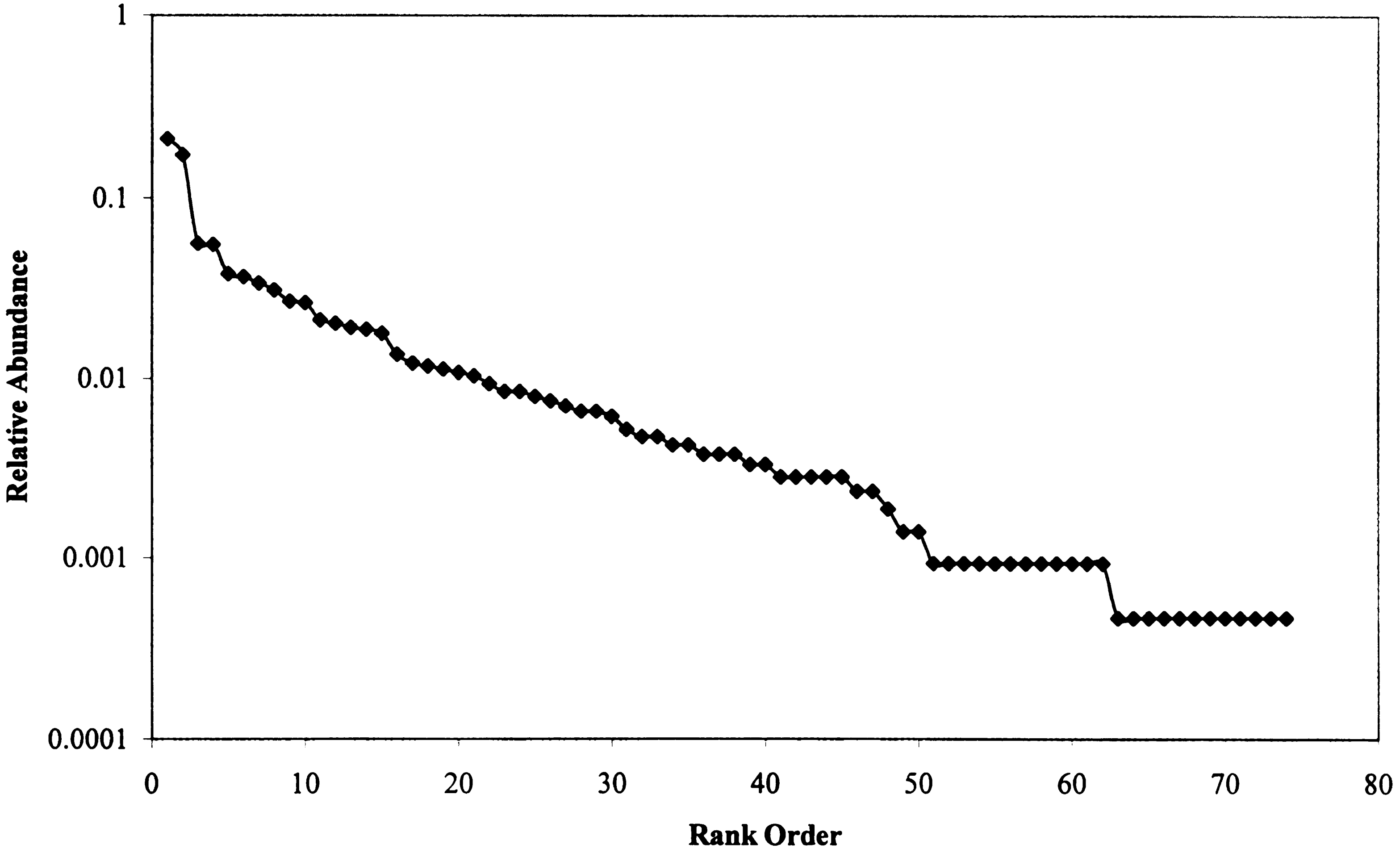


Figure B2.2: Dominance-diversity curve of Site 2, southwestern Puerto Rico

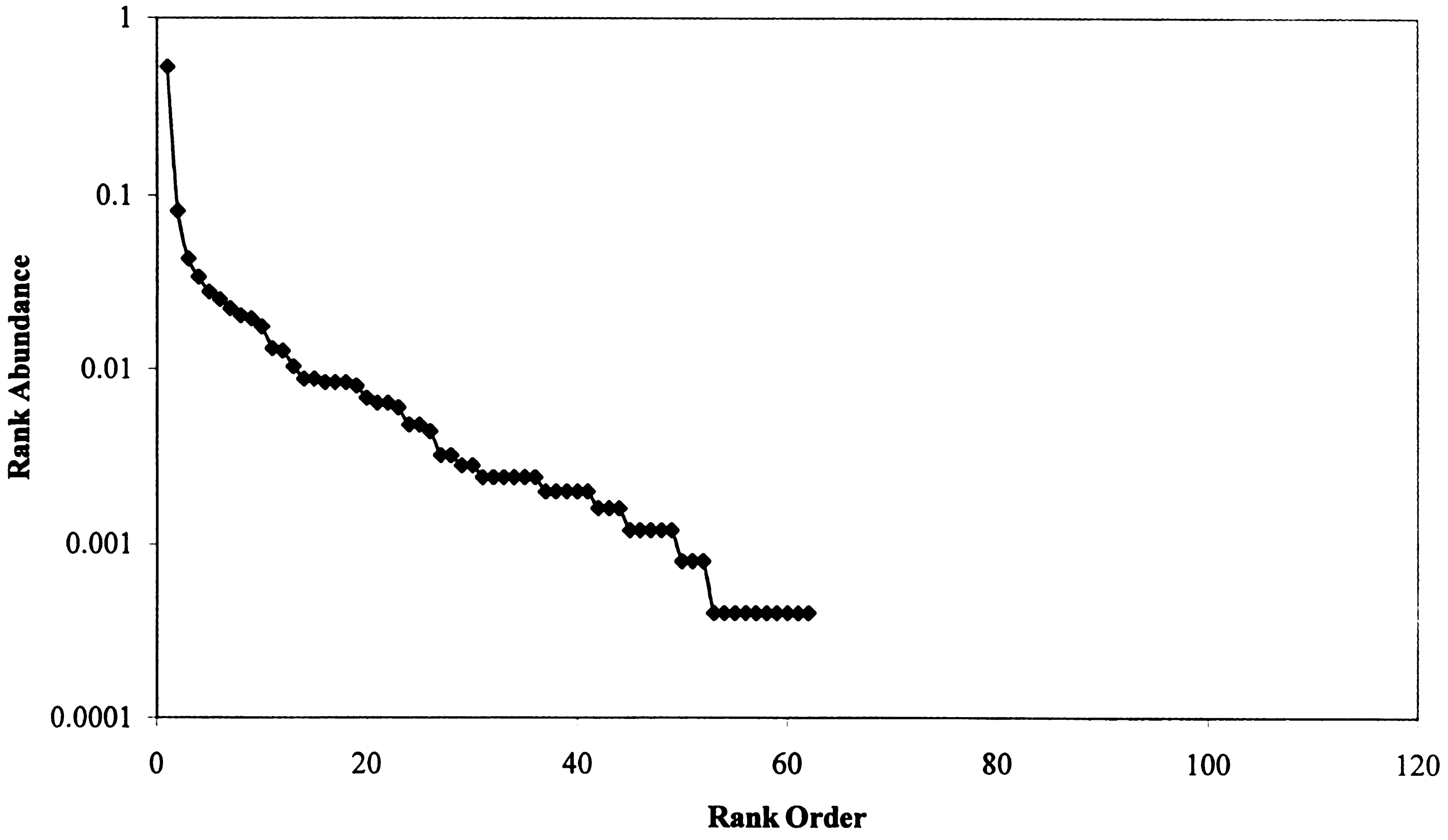


Figure B2.3: Dominance-diversity curve of Site 3, southwestern Puerto Rico

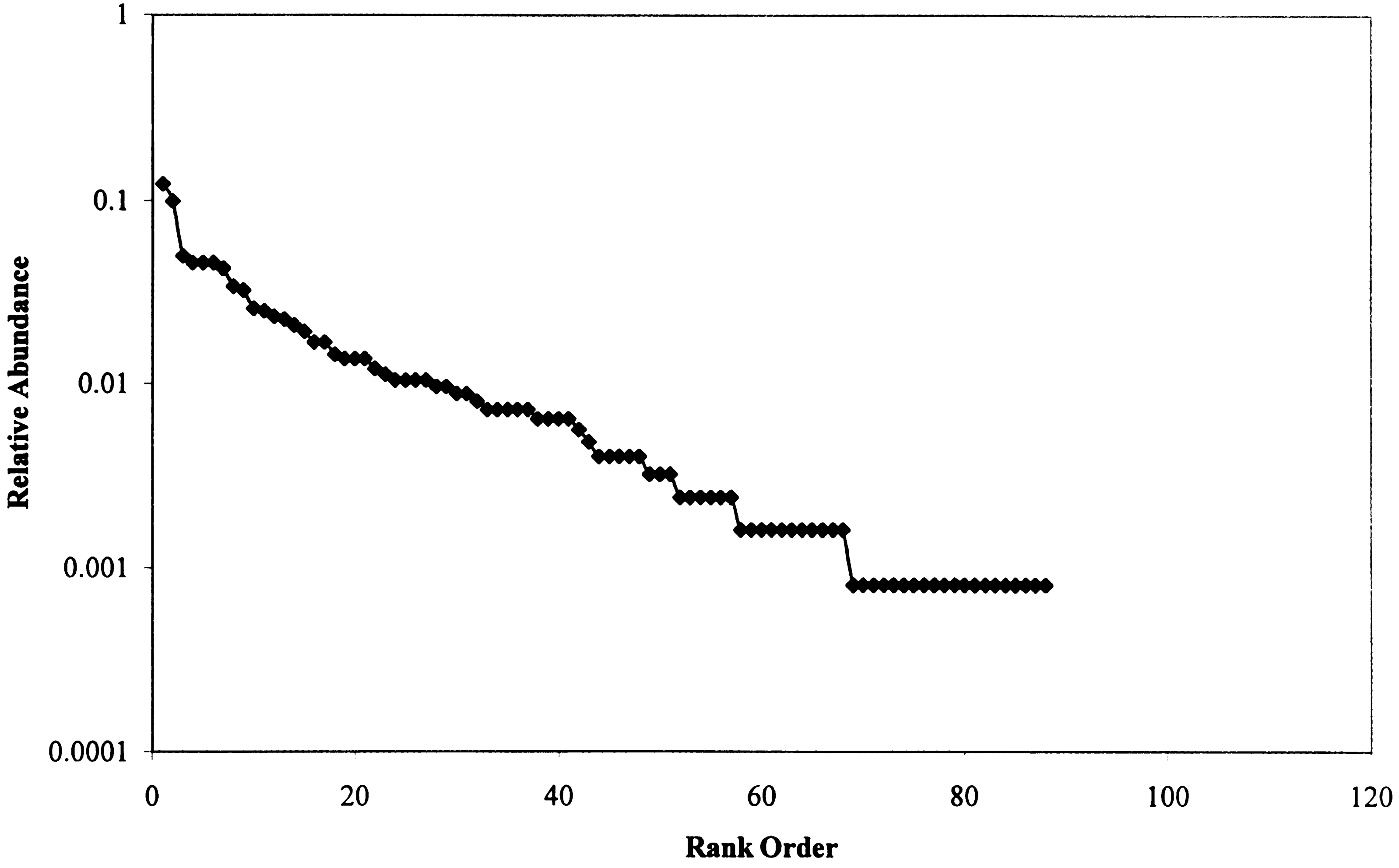


Figure B2.4: Dominance-diversity curve of Site 4, southwestern Puerto Rico

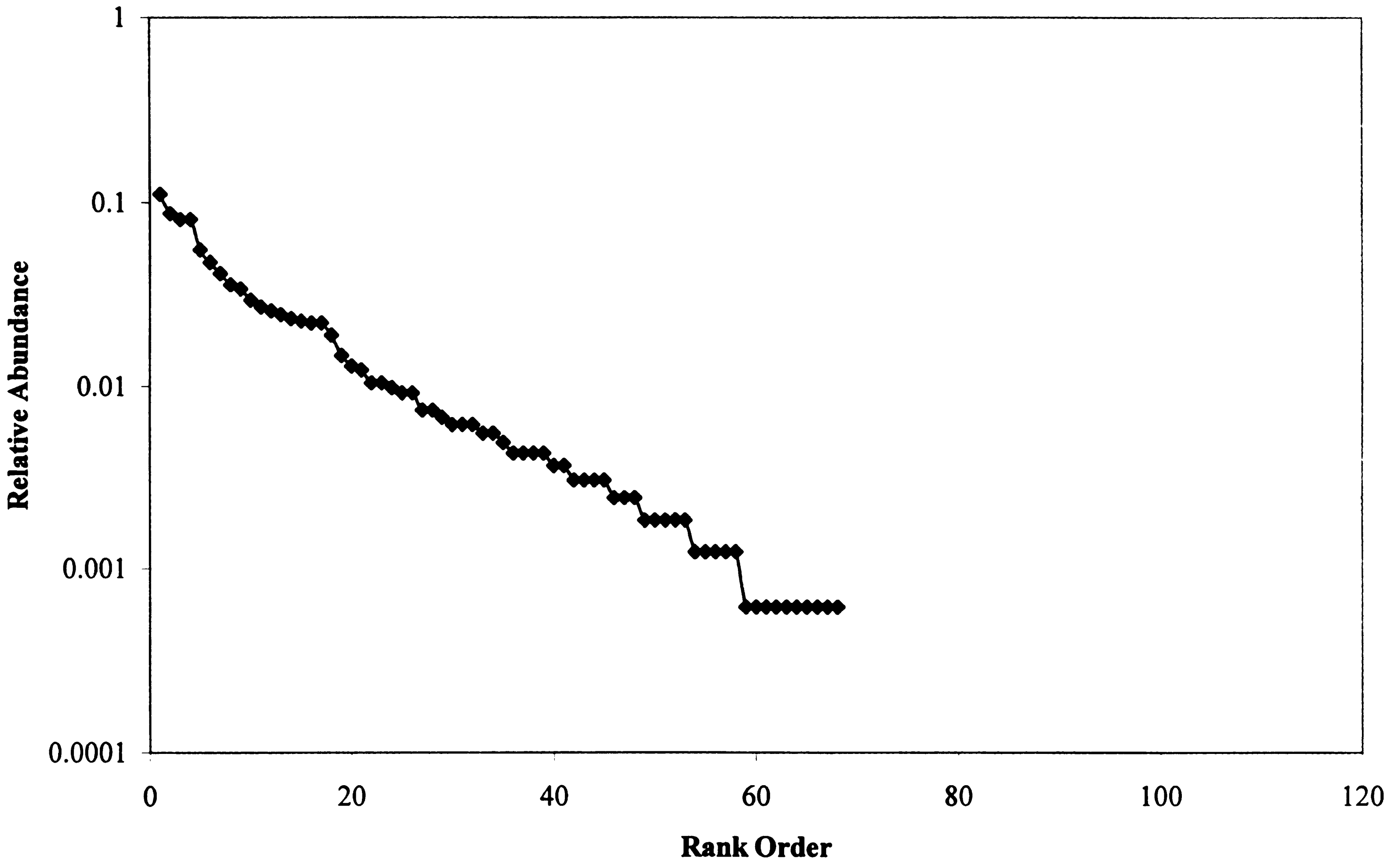


Figure B2.5: Dominance-diversity curve of Site 5, southwestern Puerto Rico

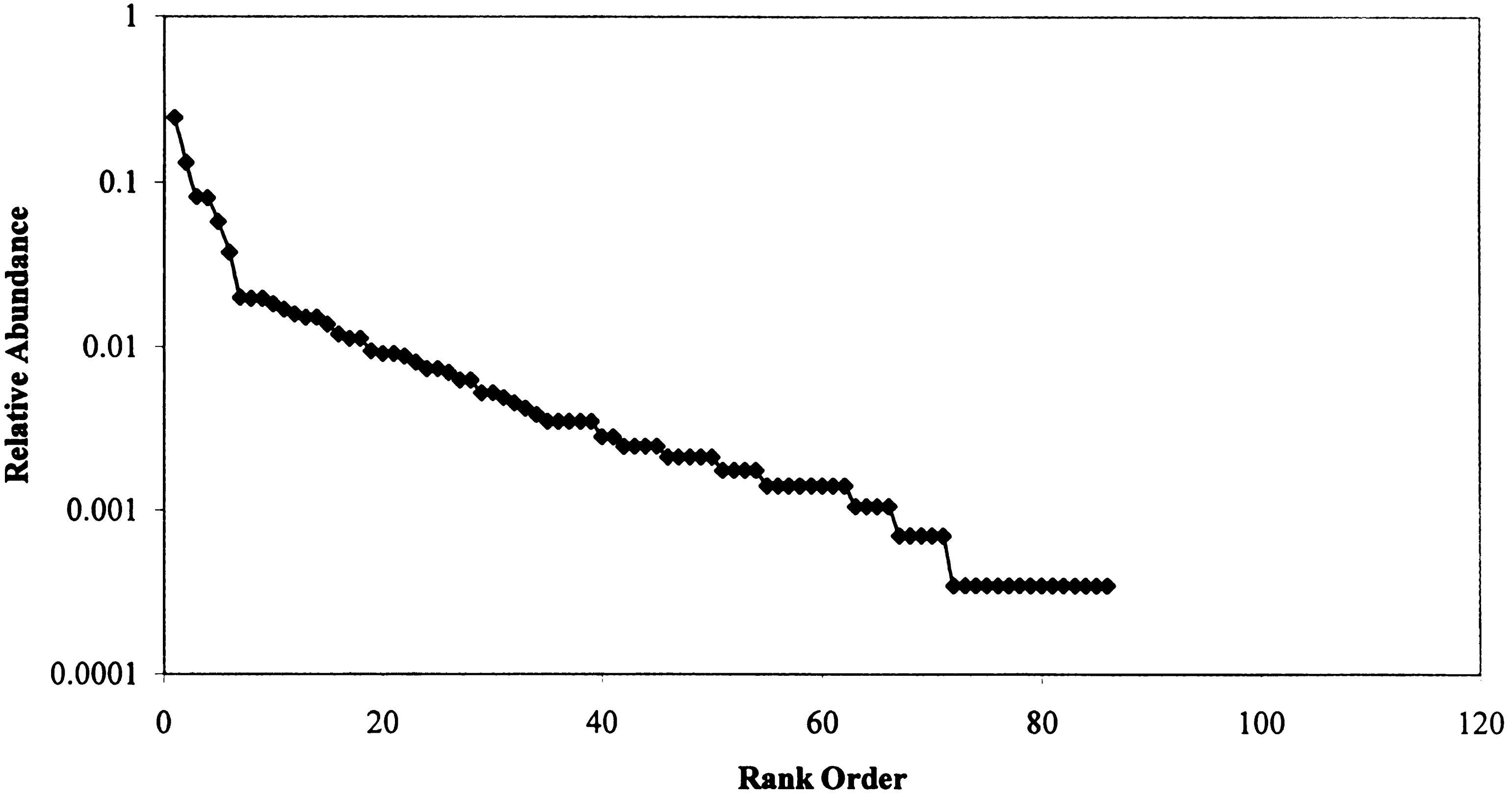


Figure B2.6: Dominance-diversity curve of Site 6, southwestern Puerto Rico

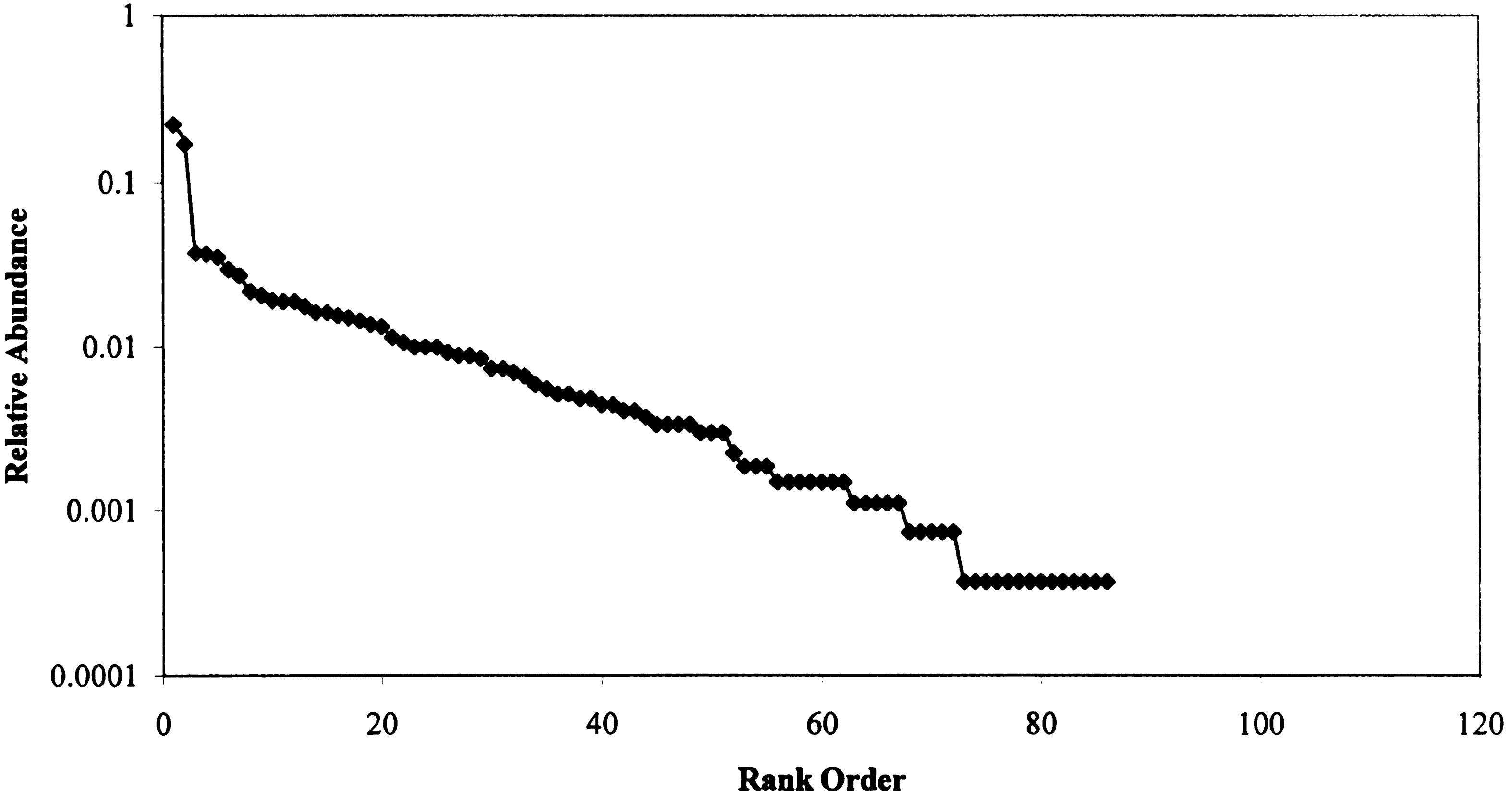


Figure B2.7: Dominance-diversity curve of Site 7, southwestern Puerto Rico

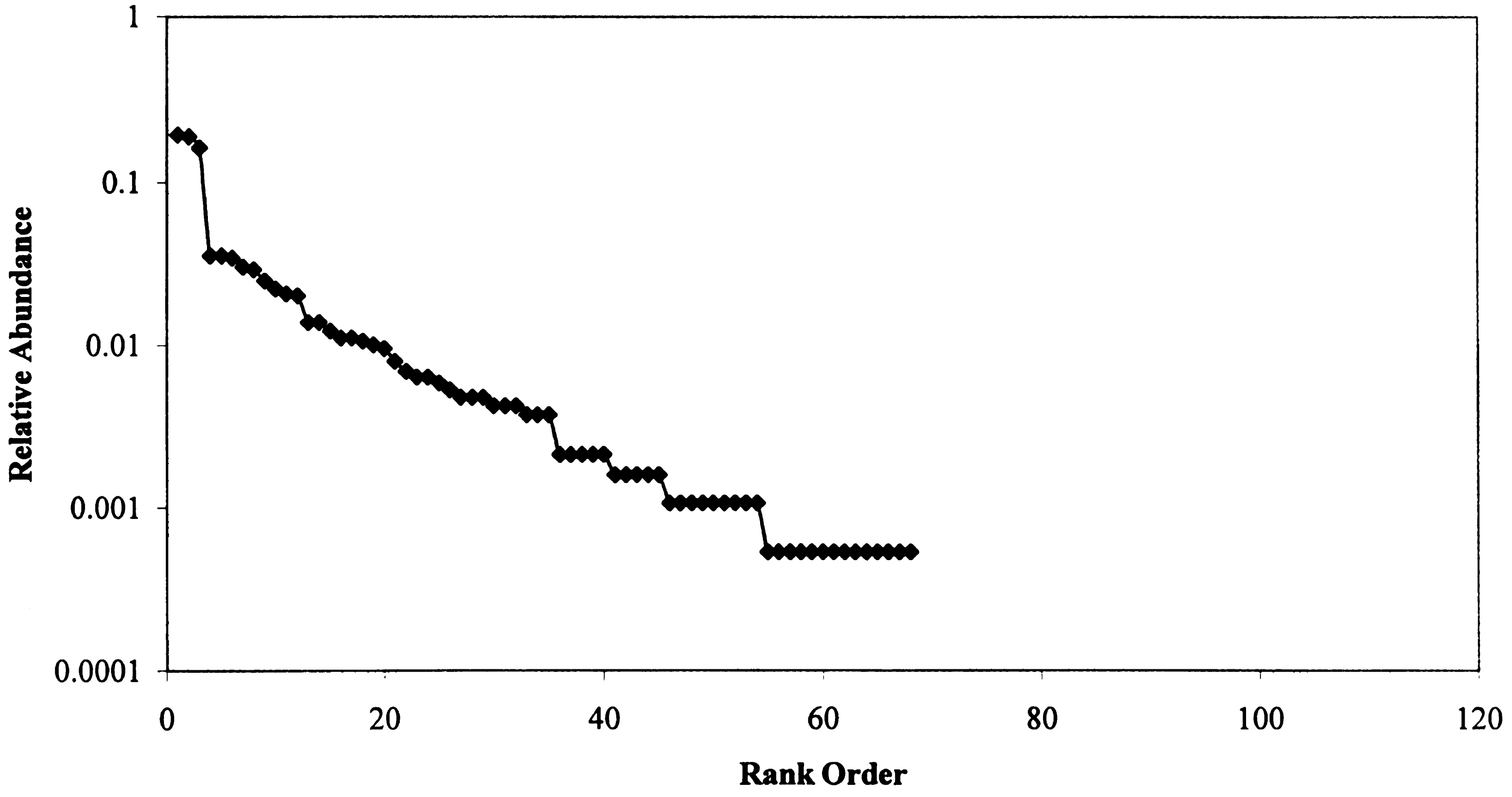


Figure B2.8: Dominance-diversity curve of Site 8, southwestern Puerto Rico

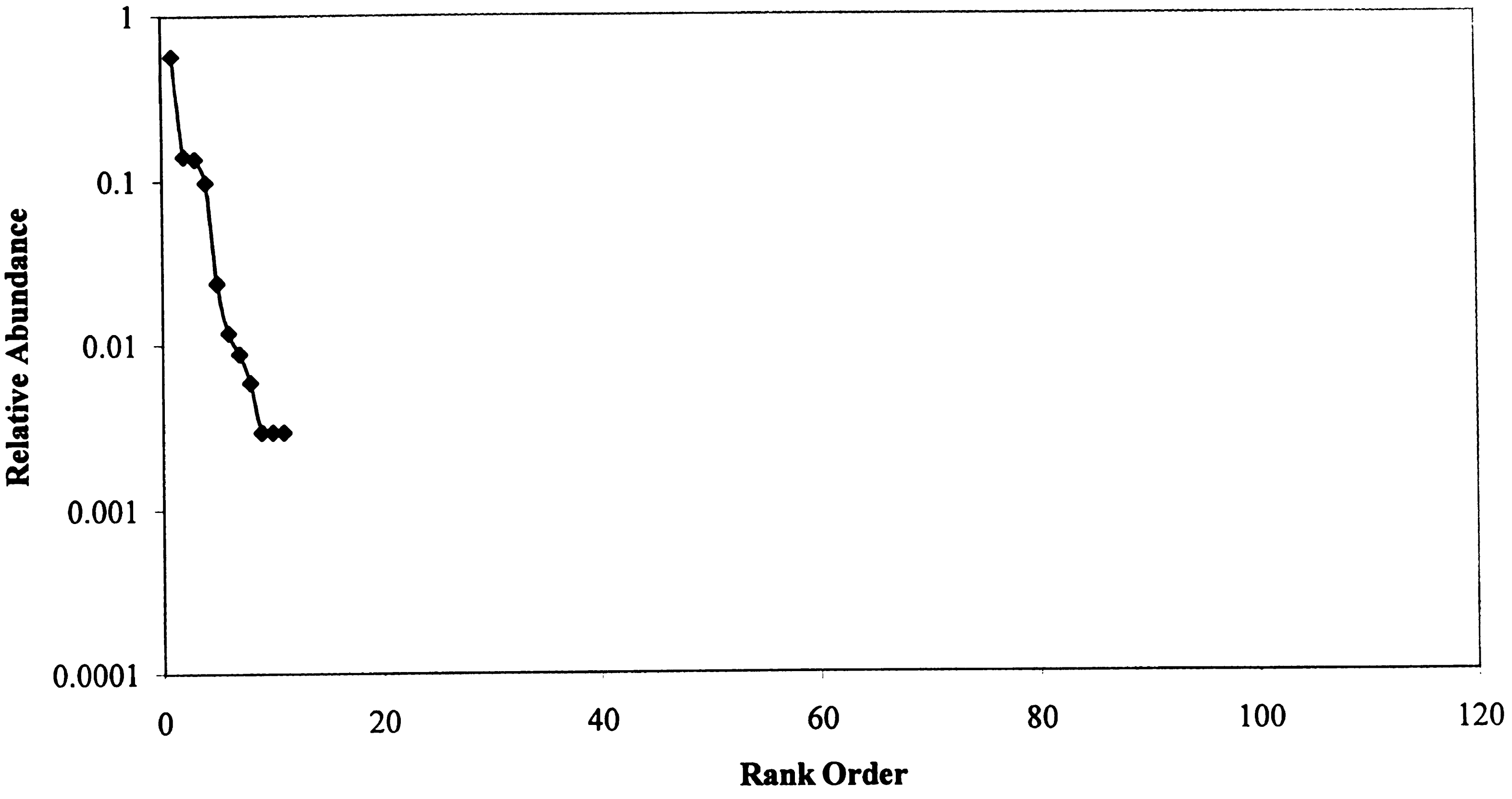


Figure B2.9: Dominance-diversity curve of Site 9, southwestern Puerto Rico

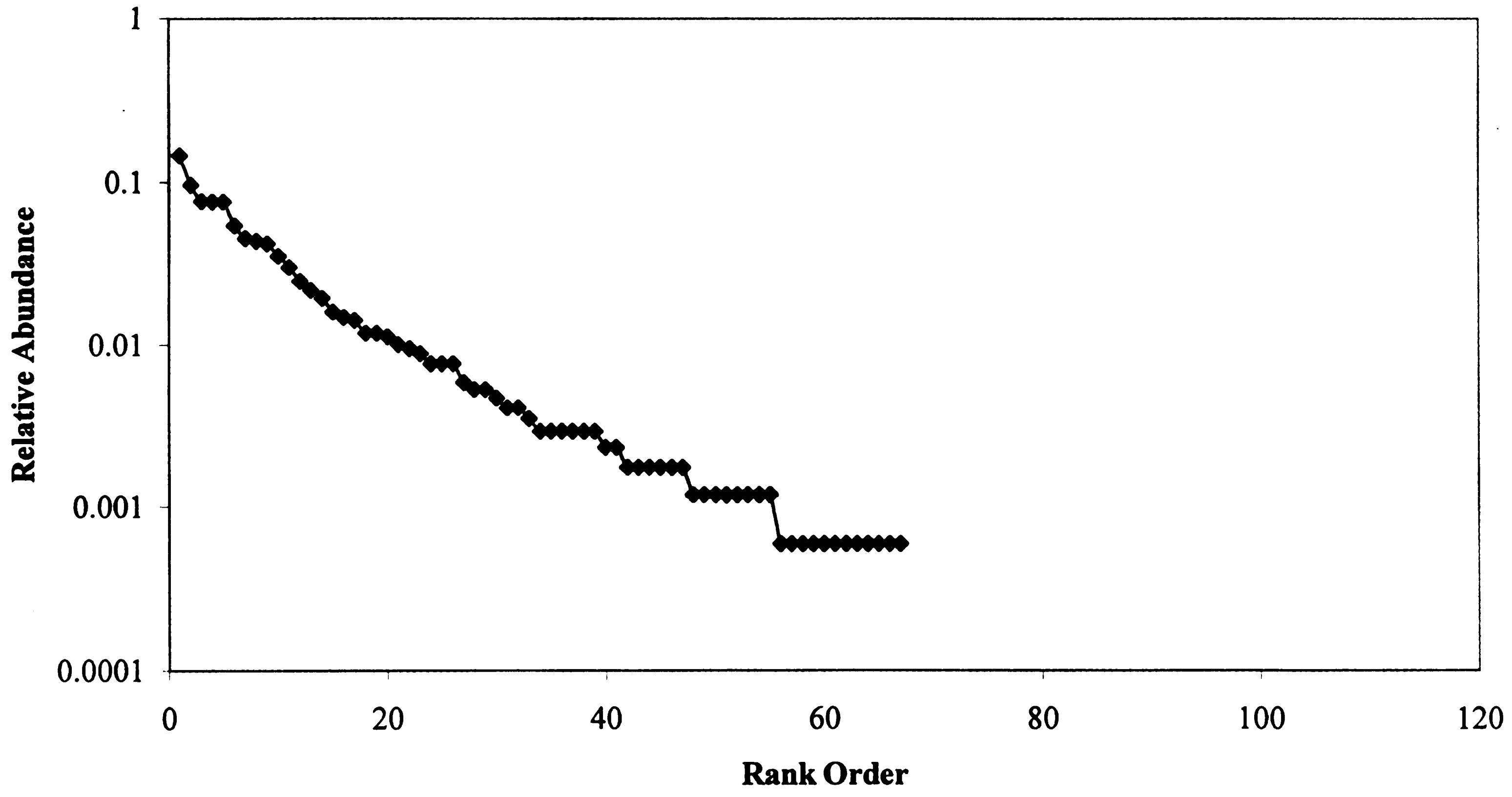


Figure B2.10: Dominance-diversity curve of Site 10, southwestern Puerto Rico

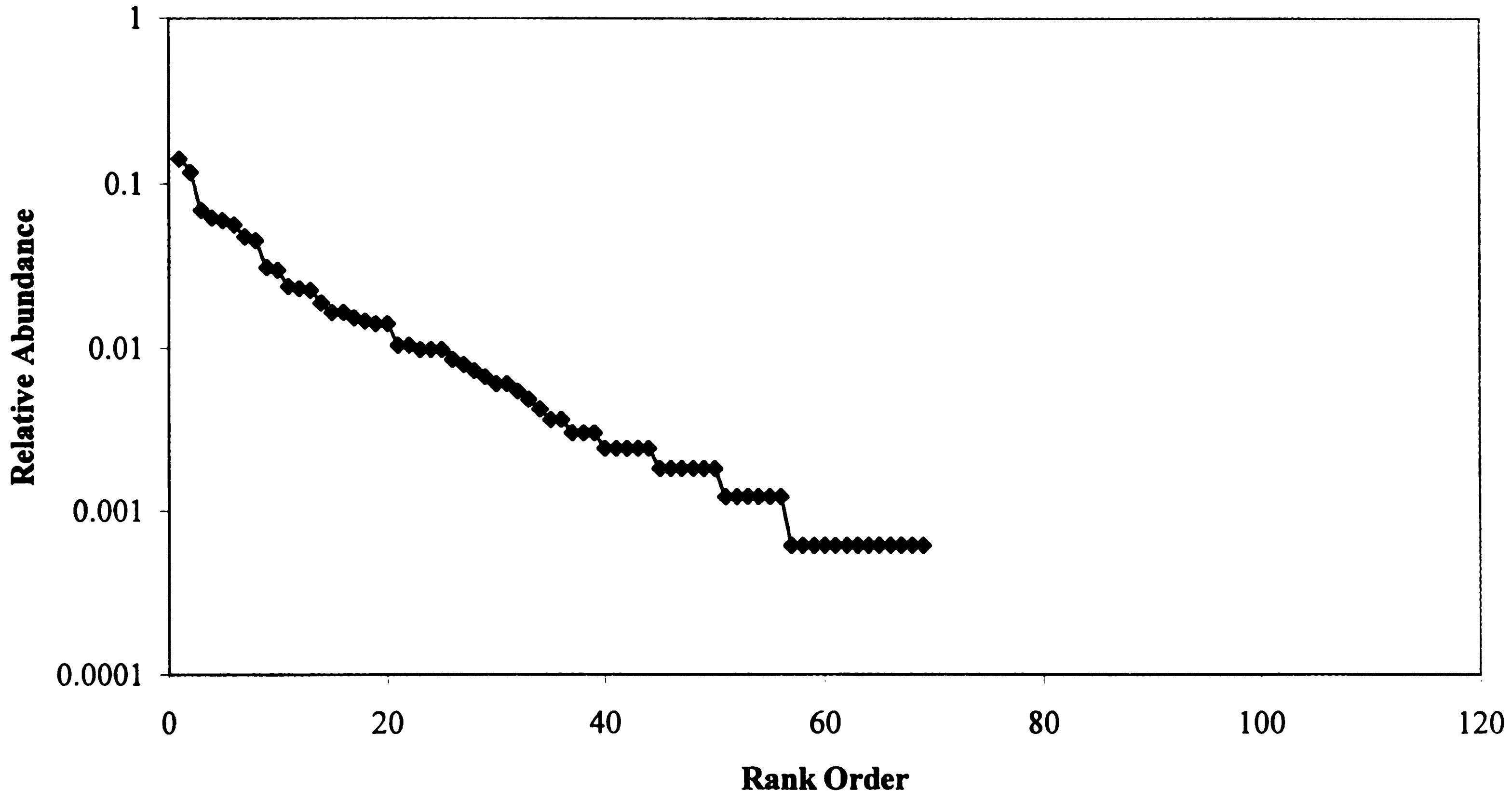


Figure B2.11: Dominance-diversity curve of Site 11, southwestern Puerto Rico

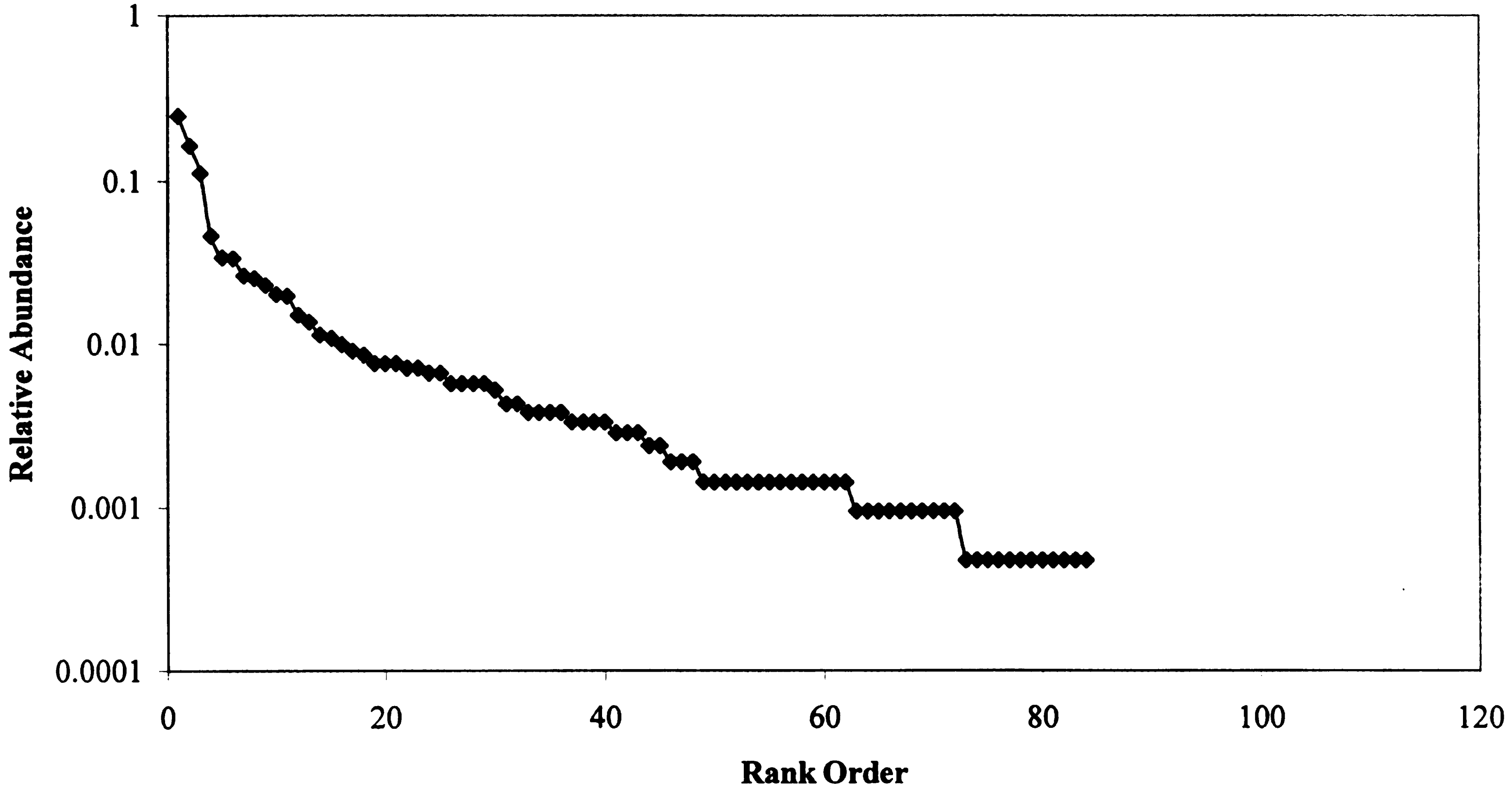


Figure B2.12: Dominance-diversity curve of Site 12, southwestern Puerto Rico

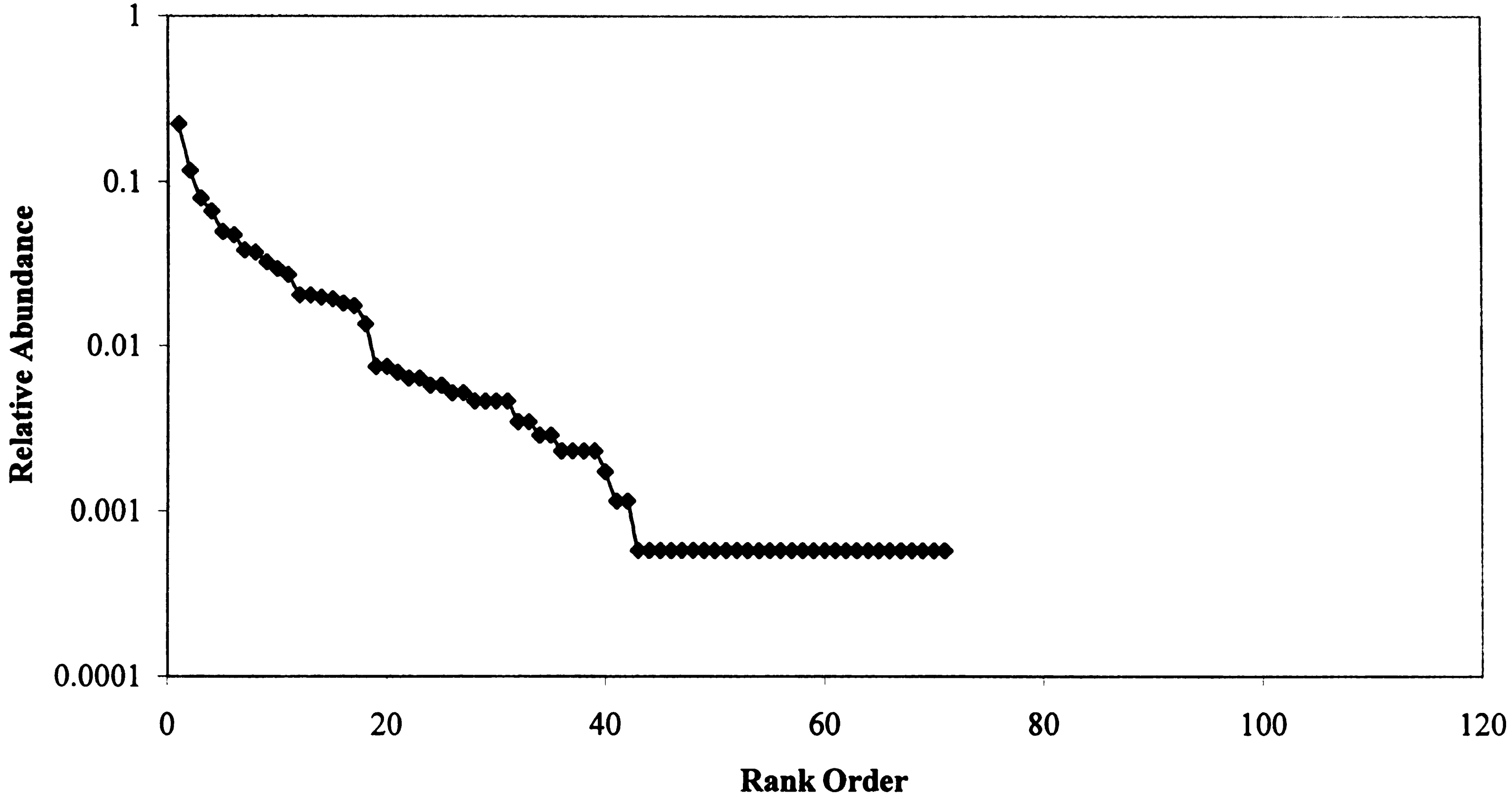


Figure B2.13: Dominance-diversity curve of Site 13, southwestern Puerto Rico

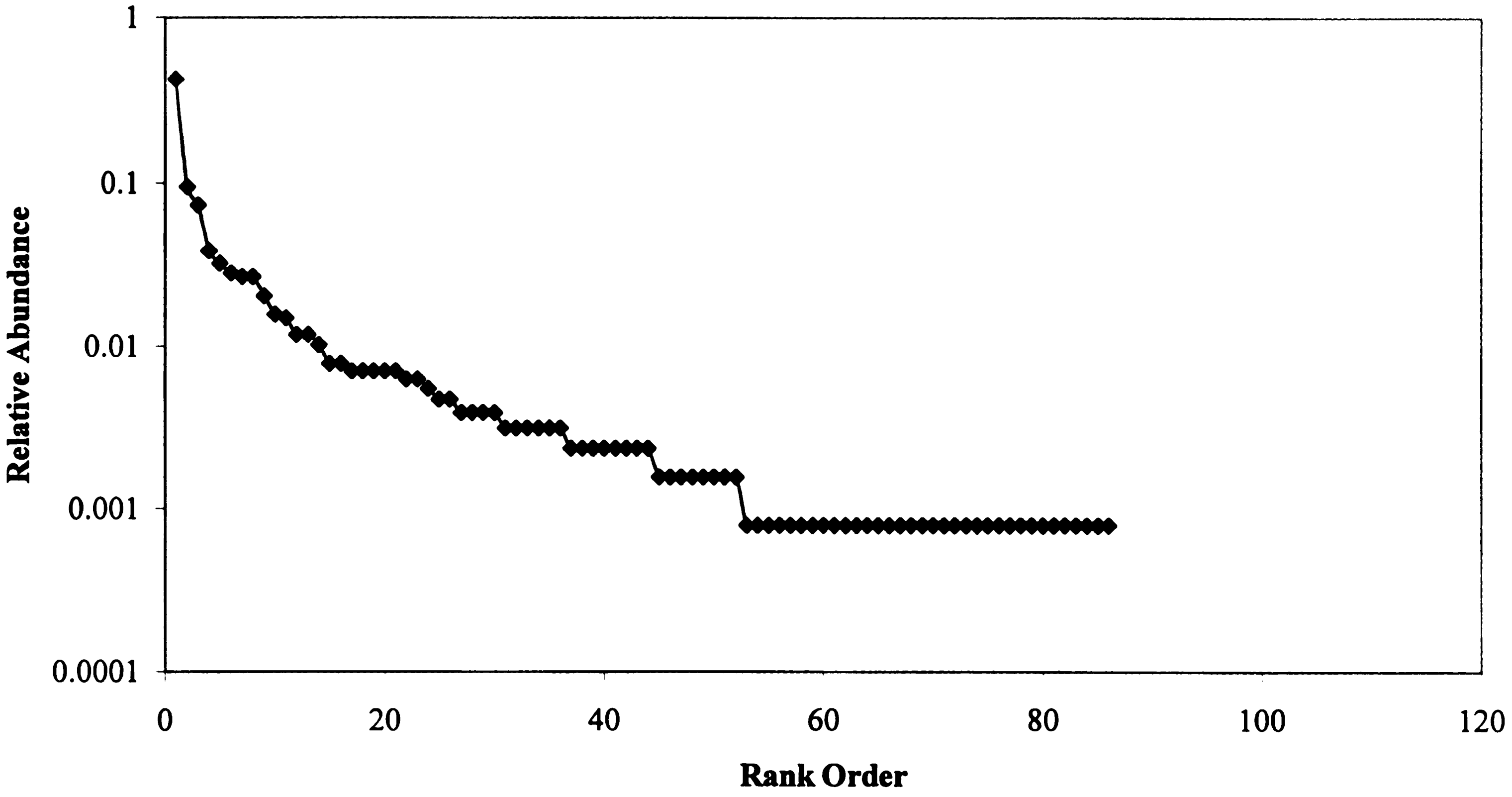


Figure B2.14: Dominance-diversity curve of Site 14, southwestern Puerto Rico

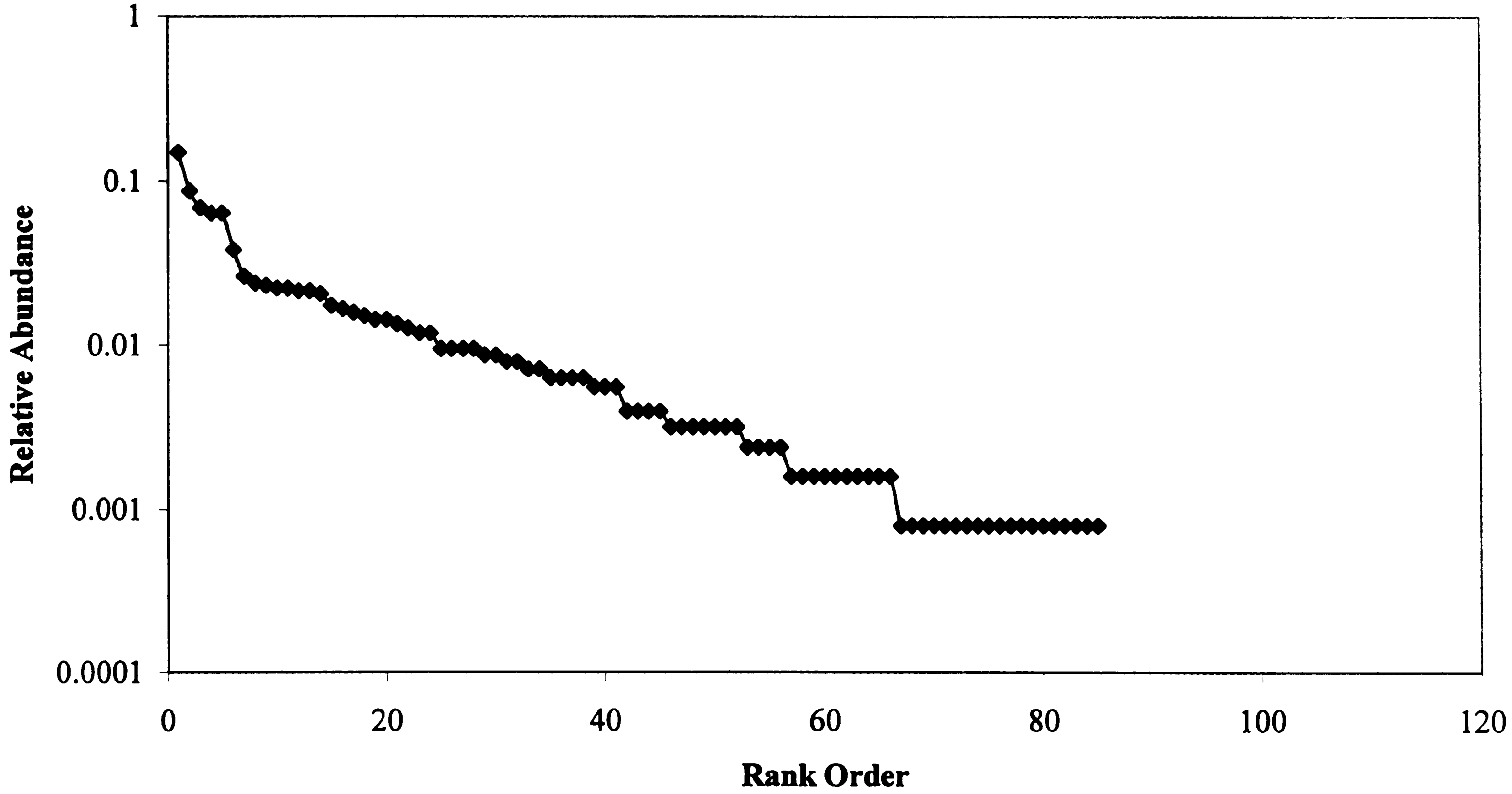


Figure B2.15: Dominance-diversity curve of Site 15, southwestern Puerto Rico

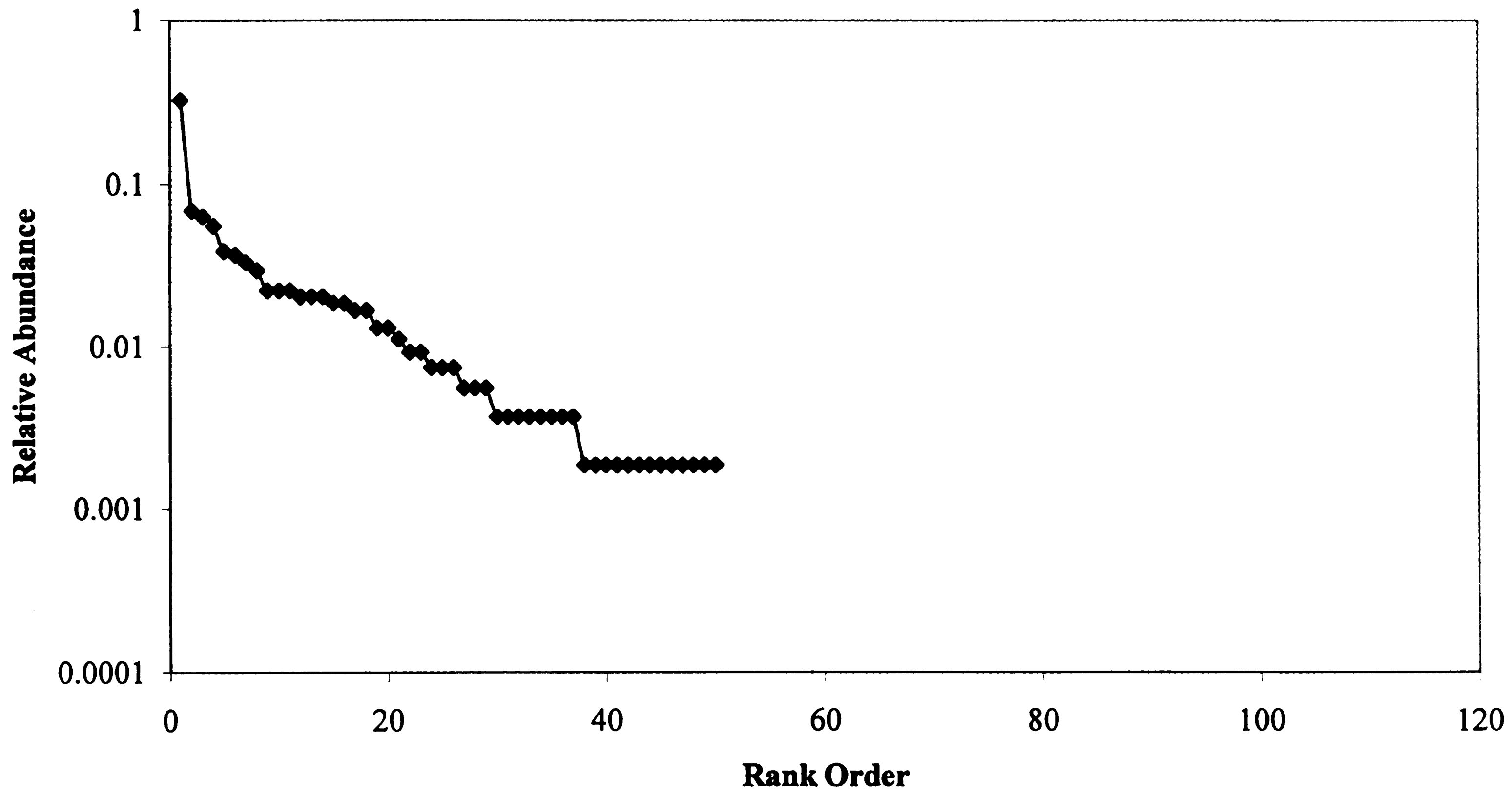


Figure B2.16: Dominance-diversity curve of Site 16, southwestern Puerto Rico

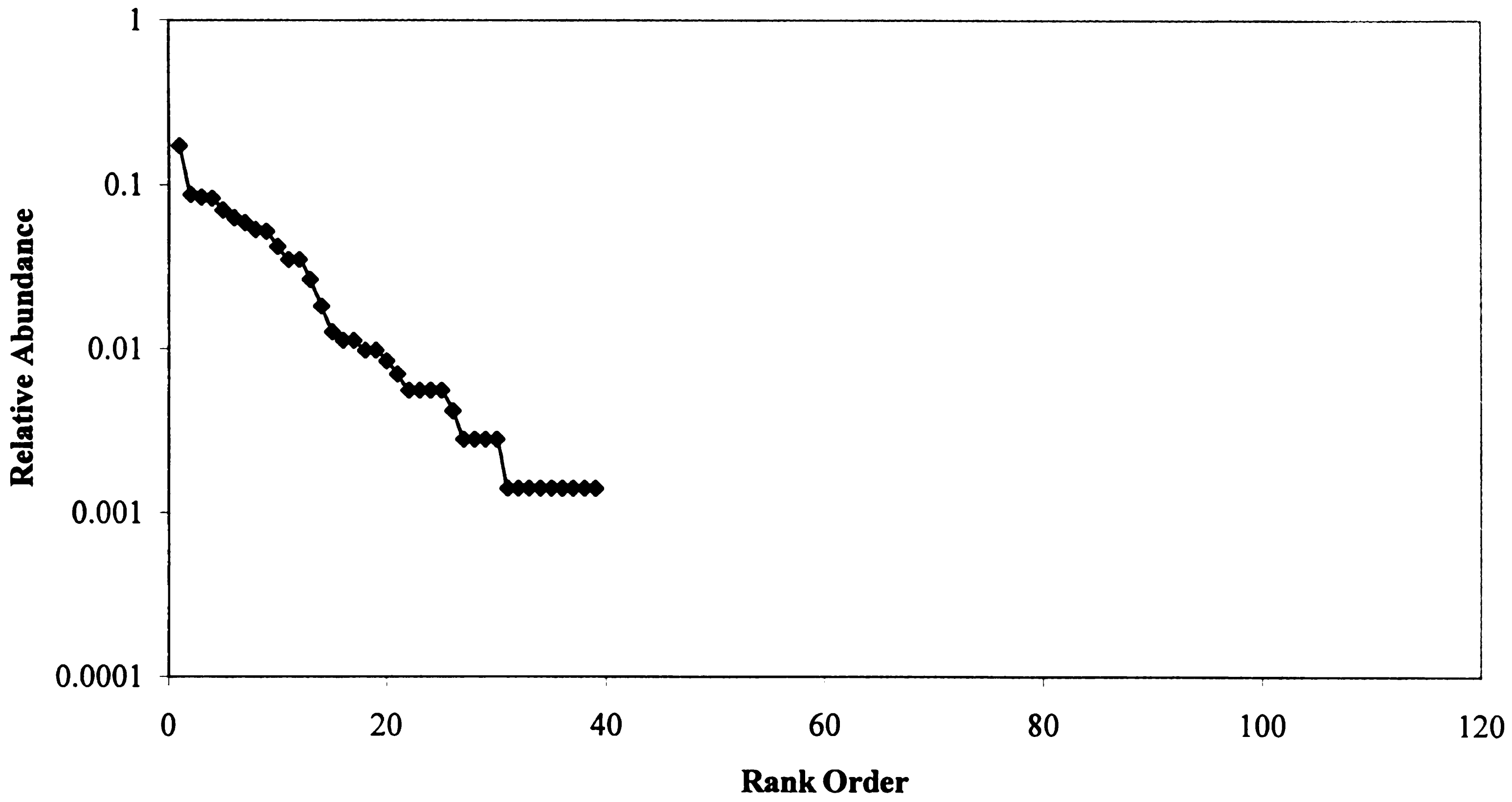


Figure B2.17: Dominance-diversity curve of Site 17, southwestern Puerto Rico

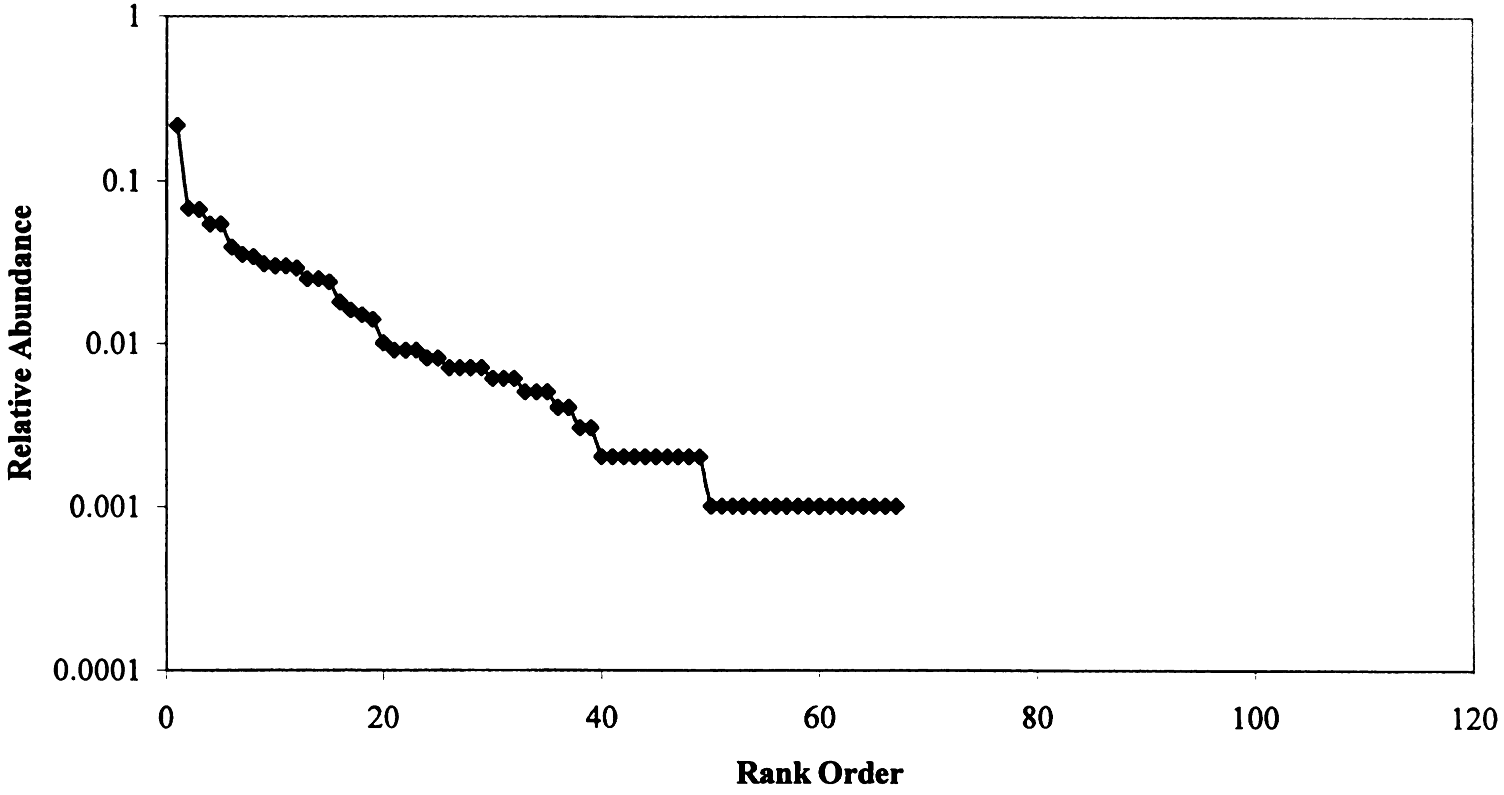


Figure B2.18: Dominance-diversity curve of Site 18, southwestern Puerto Rico

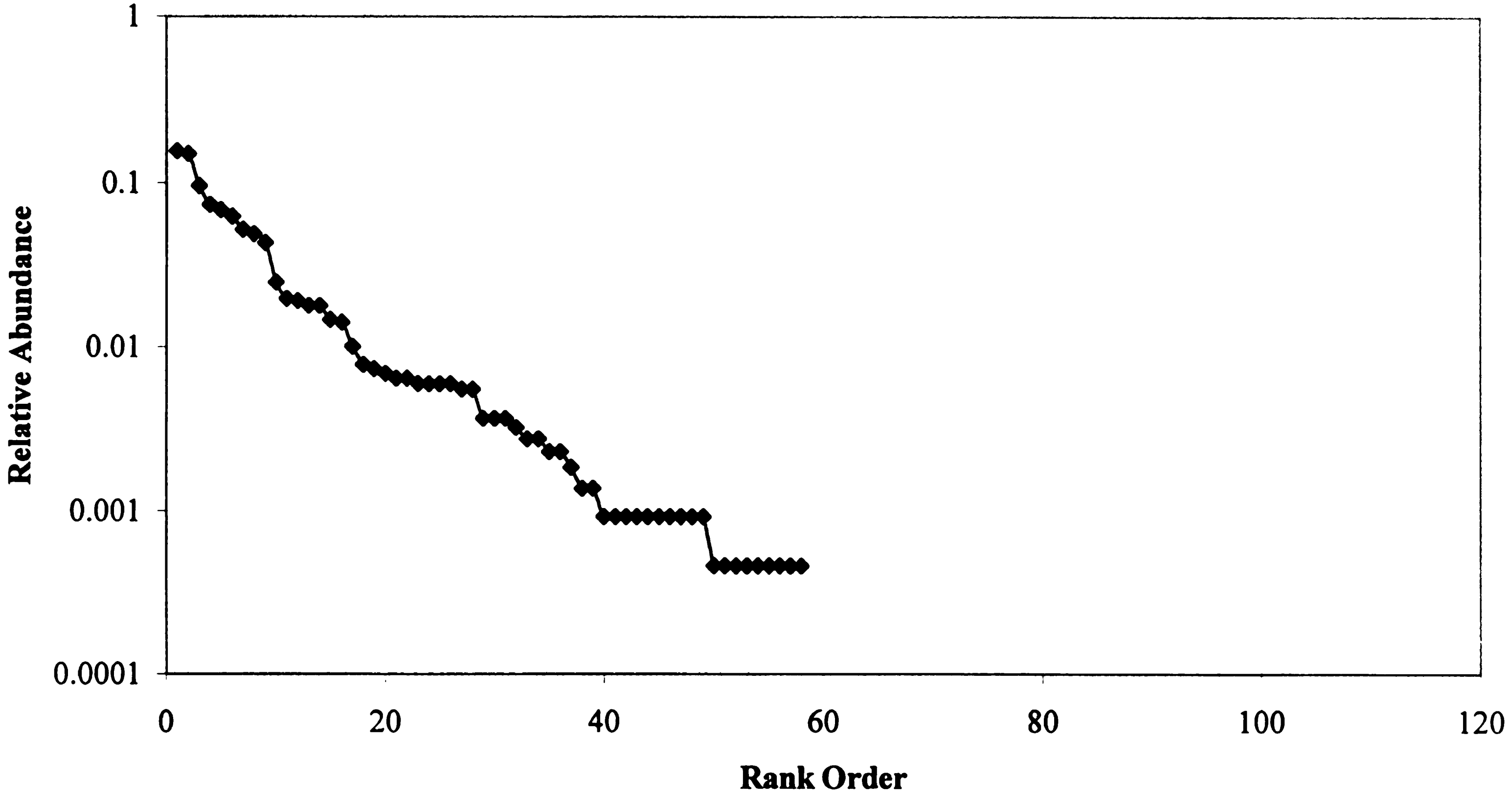


Figure B2.19: Dominance-diversity curve of Site 19, southwestern Puerto Rico

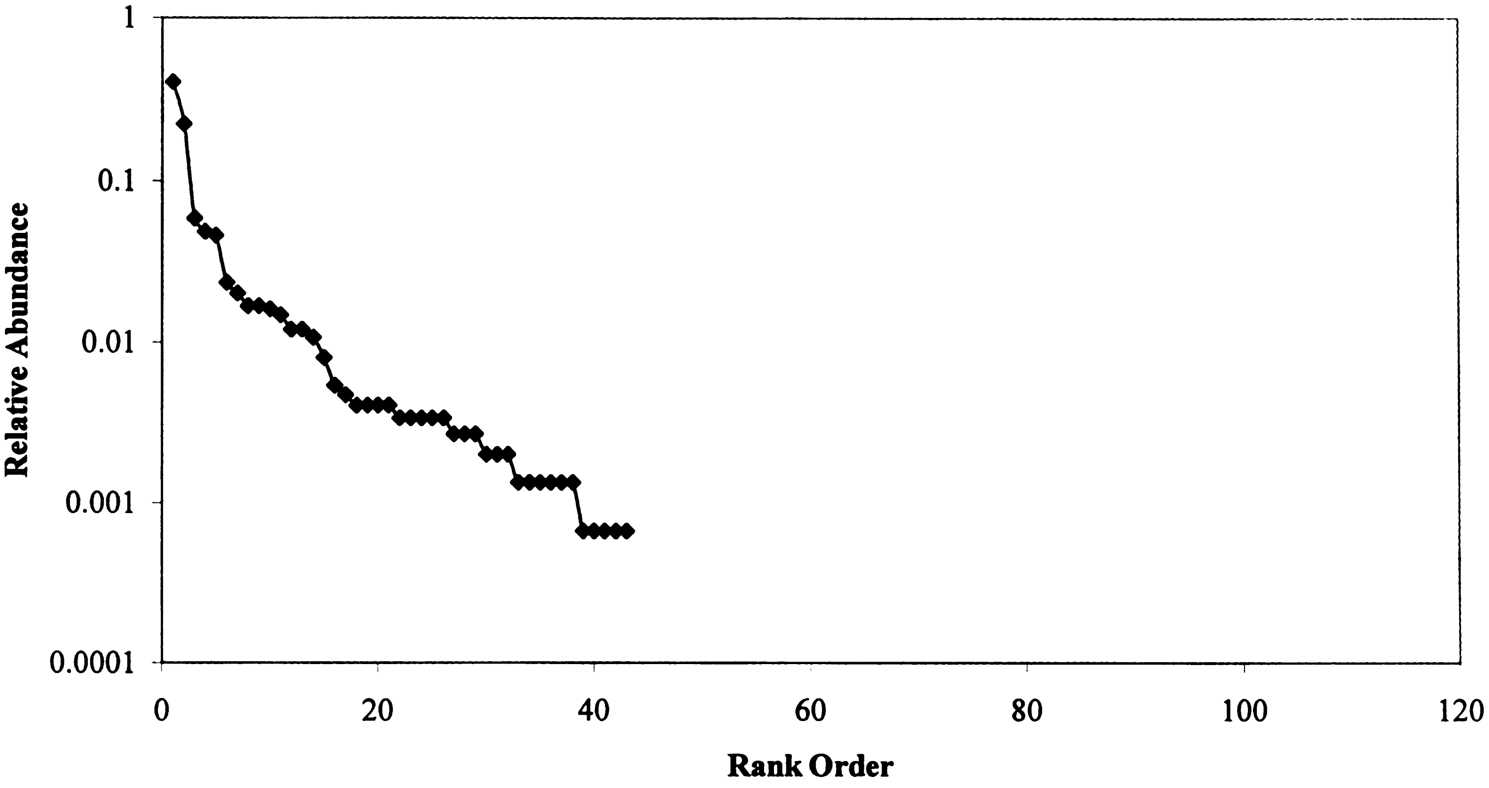


Figure B2.20: Dominance-diversity curve of Site 20, southwestern Puerto Rico

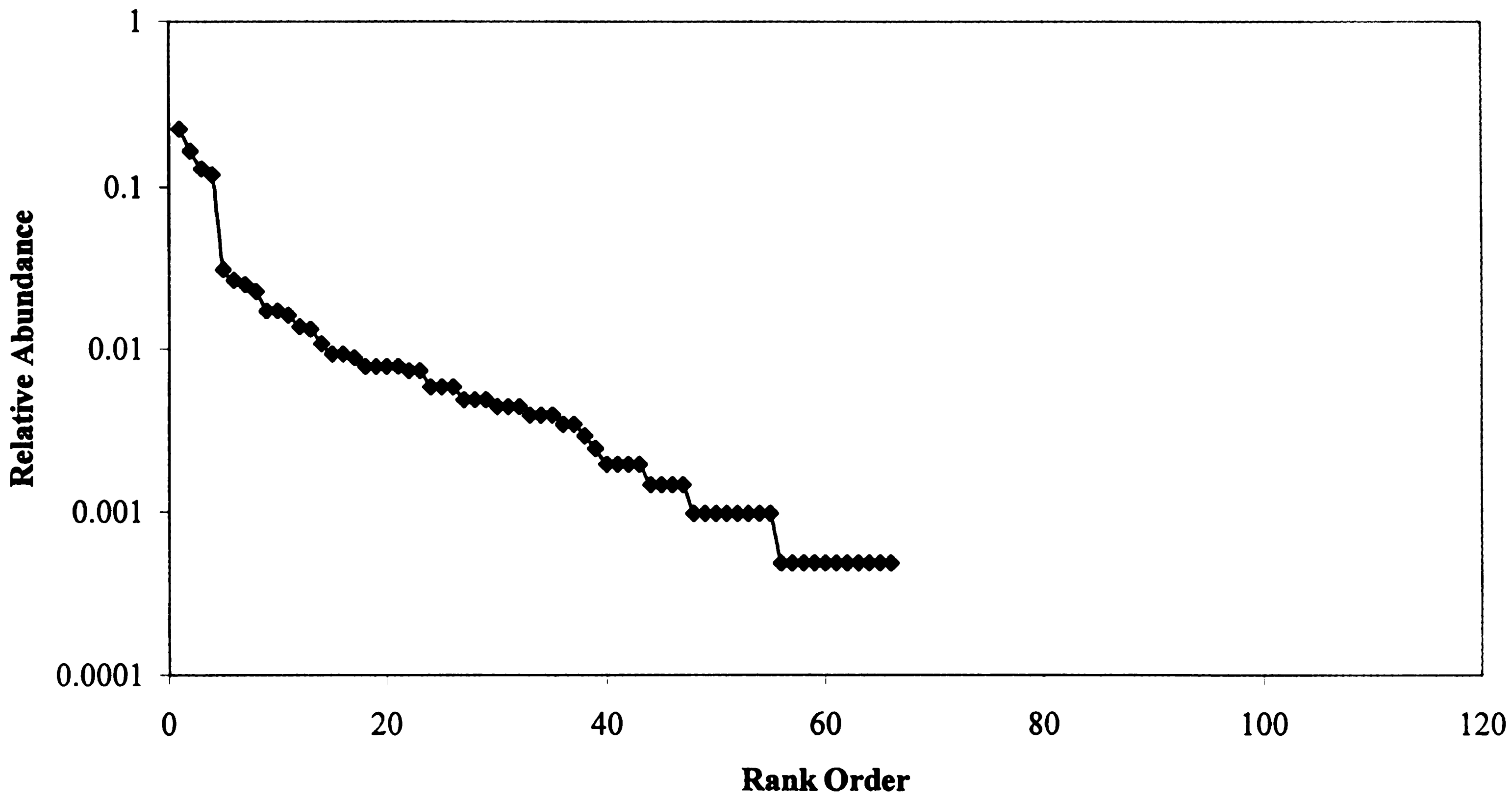


Figure B2.21: Dominance-diversity curve of Site 21, southwestern Puerto Rico

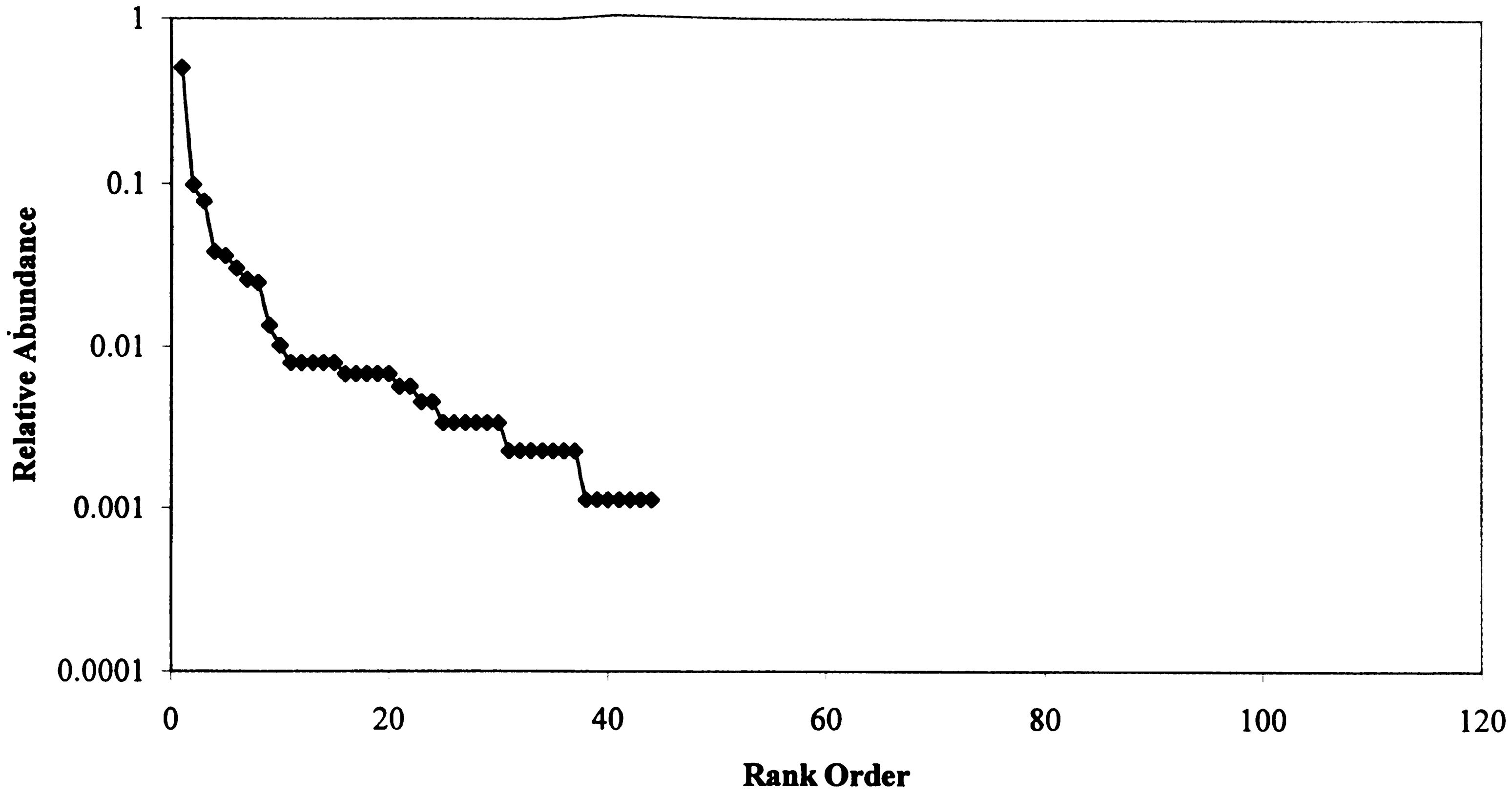


Figure B2.22: Dominance-diversity curve of Site 22, southwestern Puerto Rico

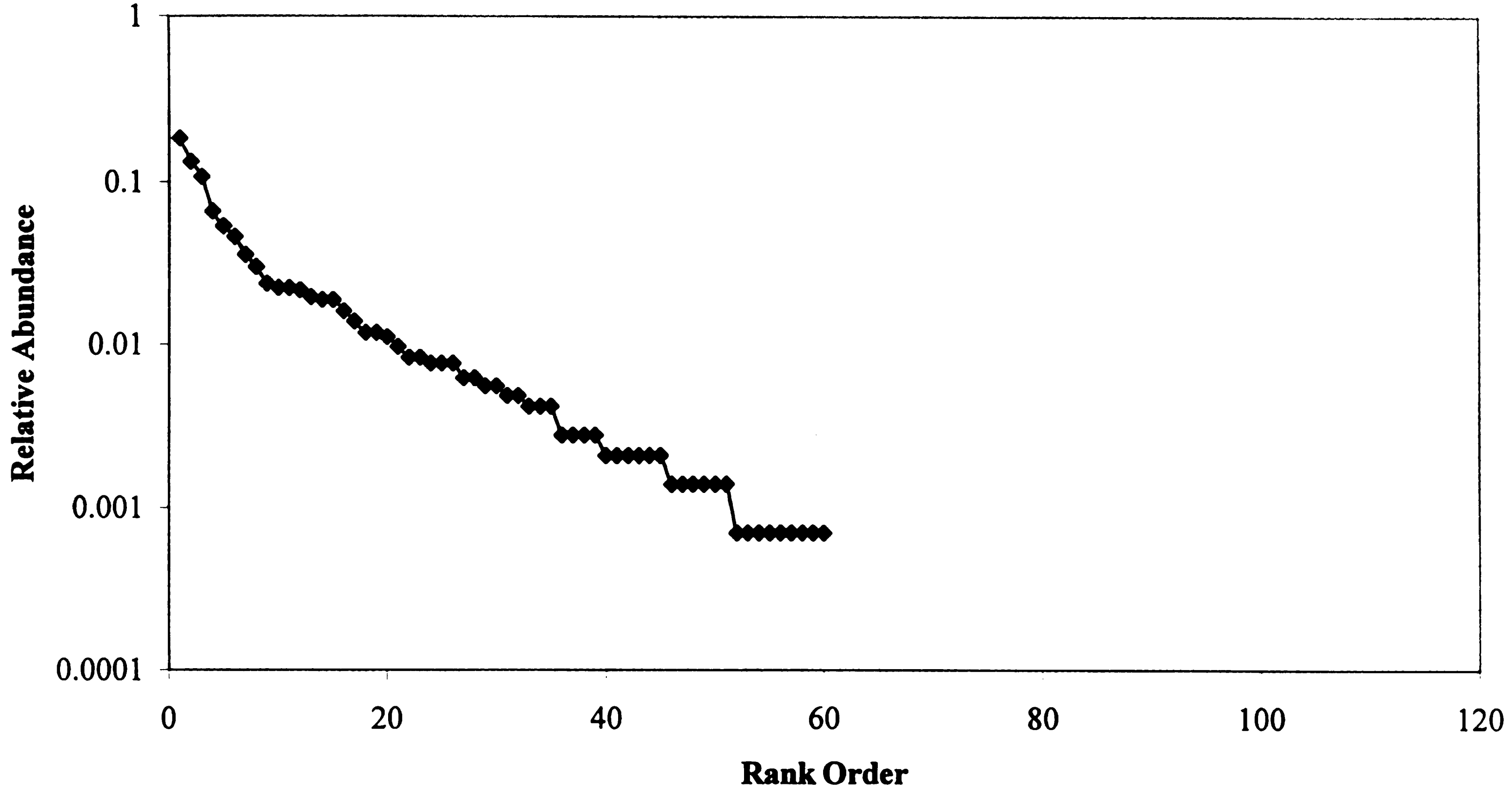


Figure B2.23: Dominance-diversity curve of Site 23, southwestern Puerto Rico

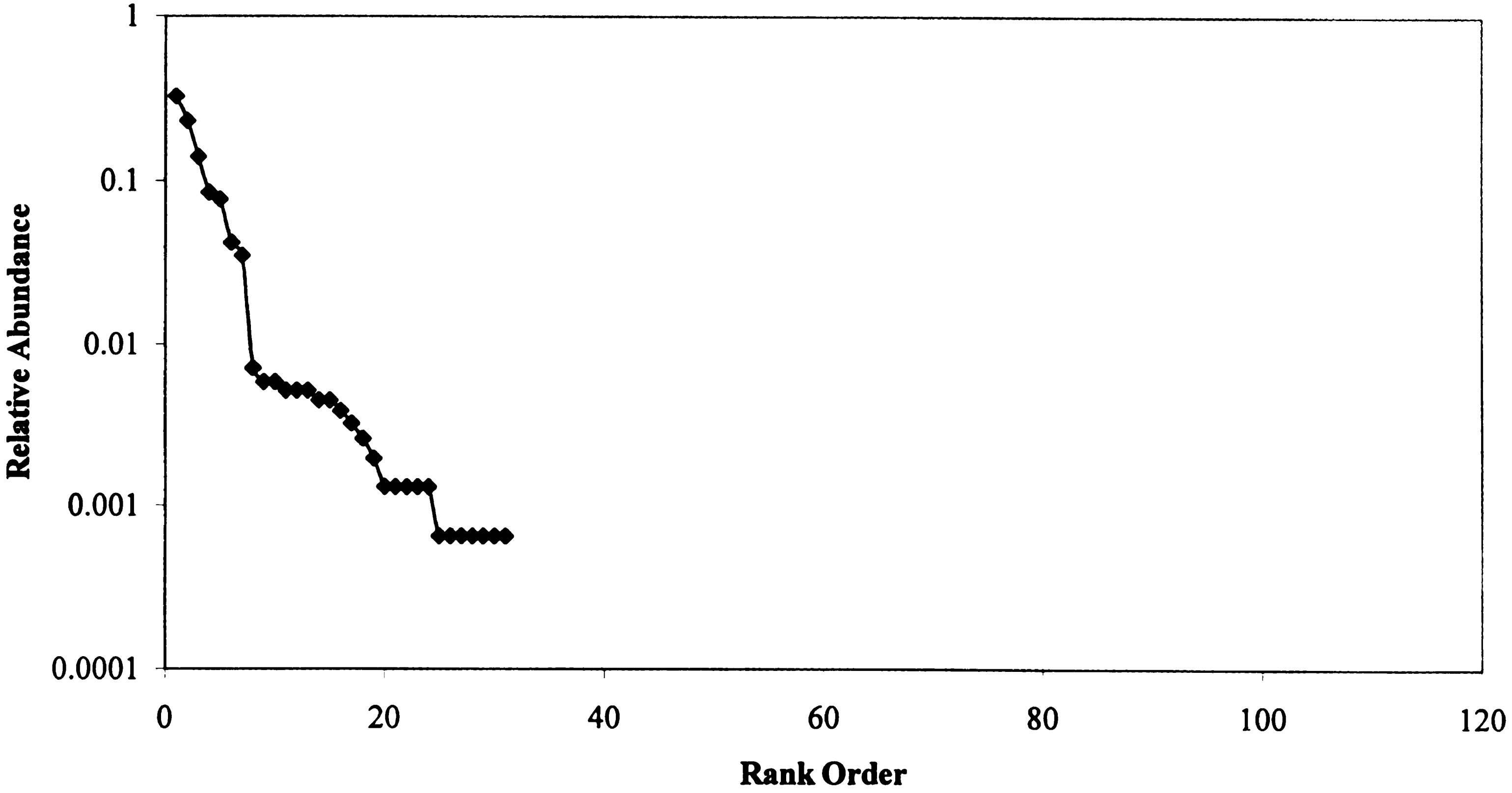


Figure B2.24: Dominance-diversity curve of Site 24, southwestern Puerto Rico

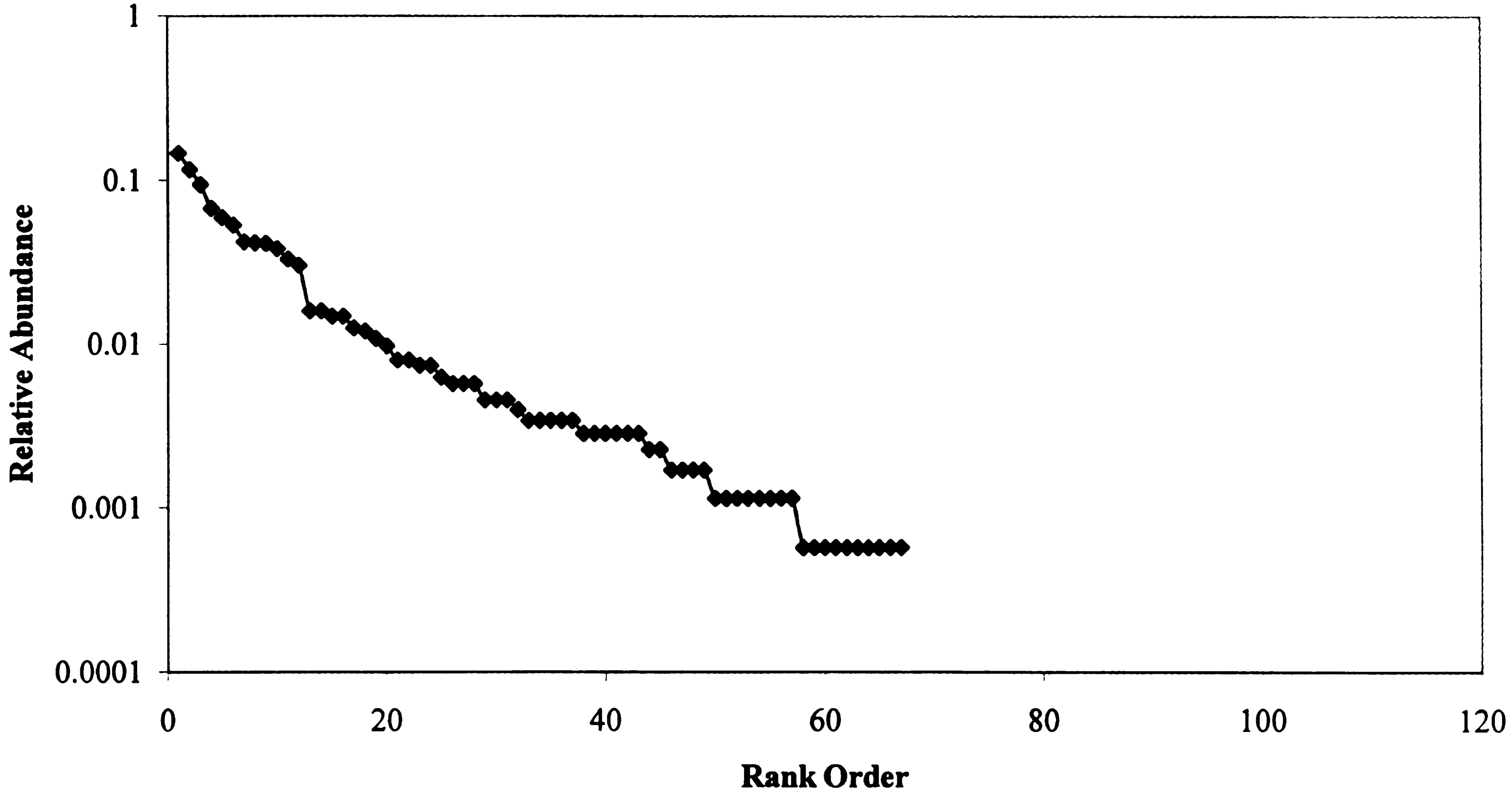


Figure B2.25: Dominance-diversity curve of Site 25, southwestern Puerto Rico

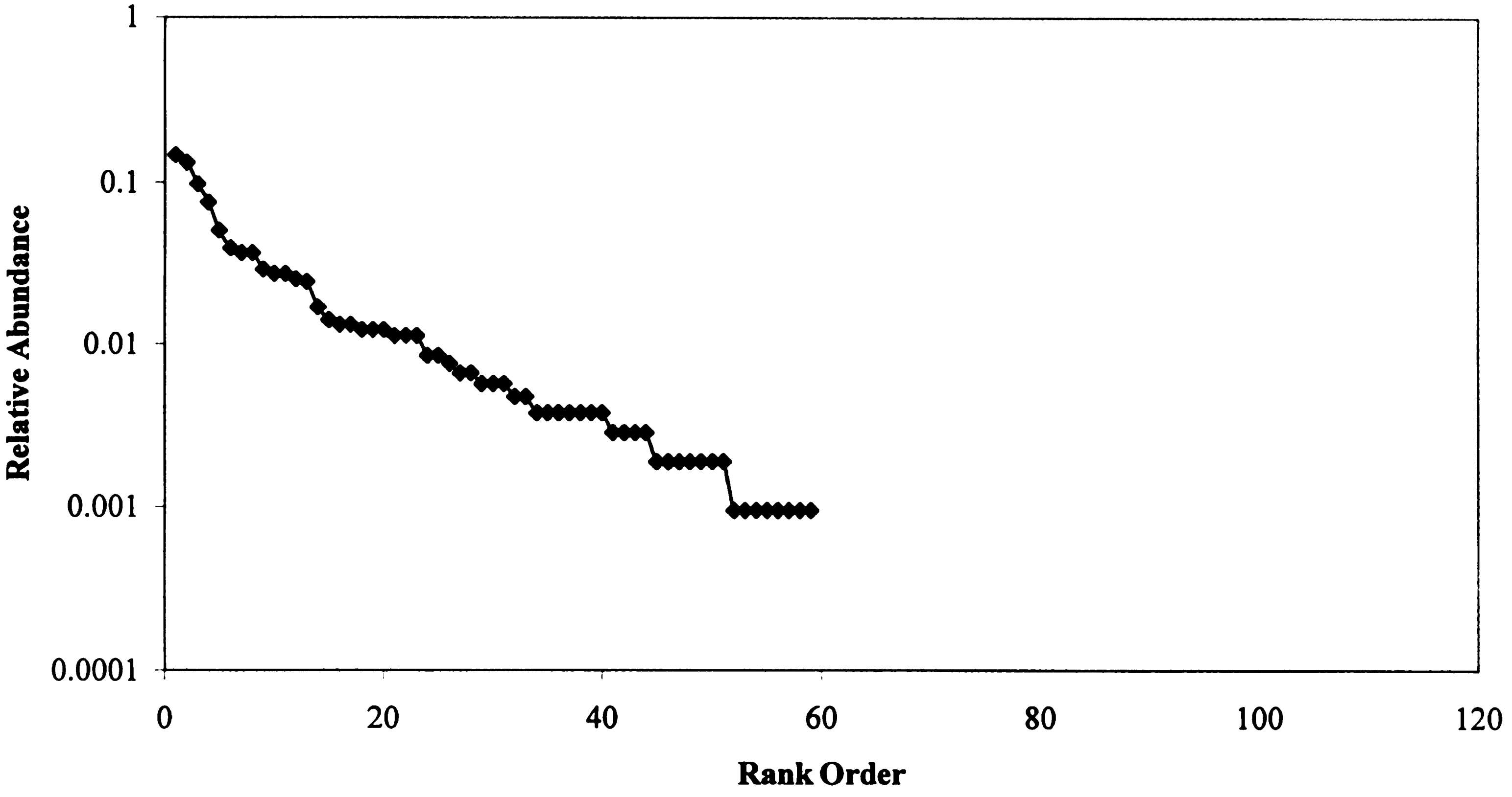


Figure B2.26: Dominance-diversity curve of Site 26, southwestern Puerto Rico

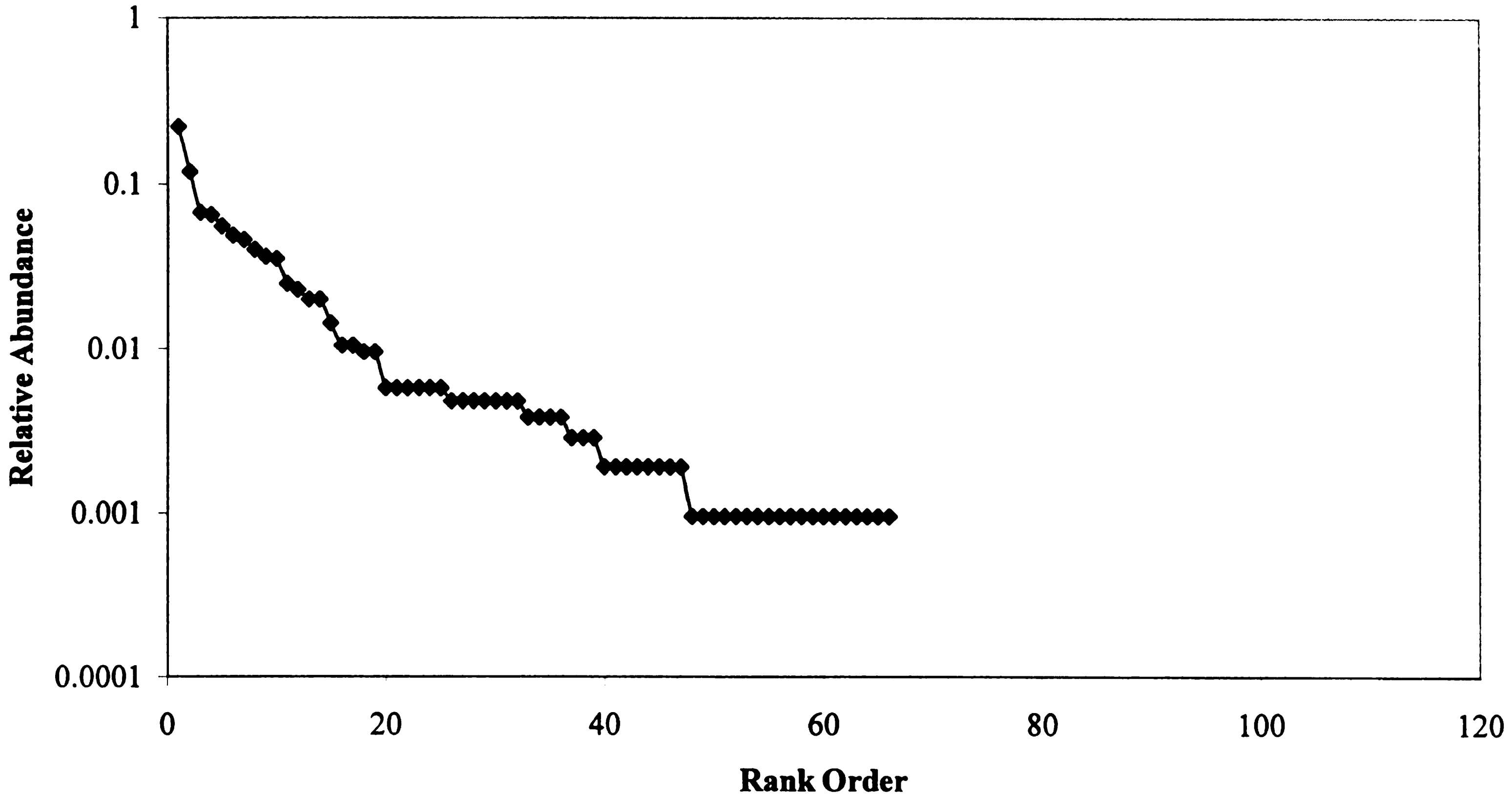


Figure B2.27: Dominance-diversity curve of Site 27, southwestern Puerto Rico

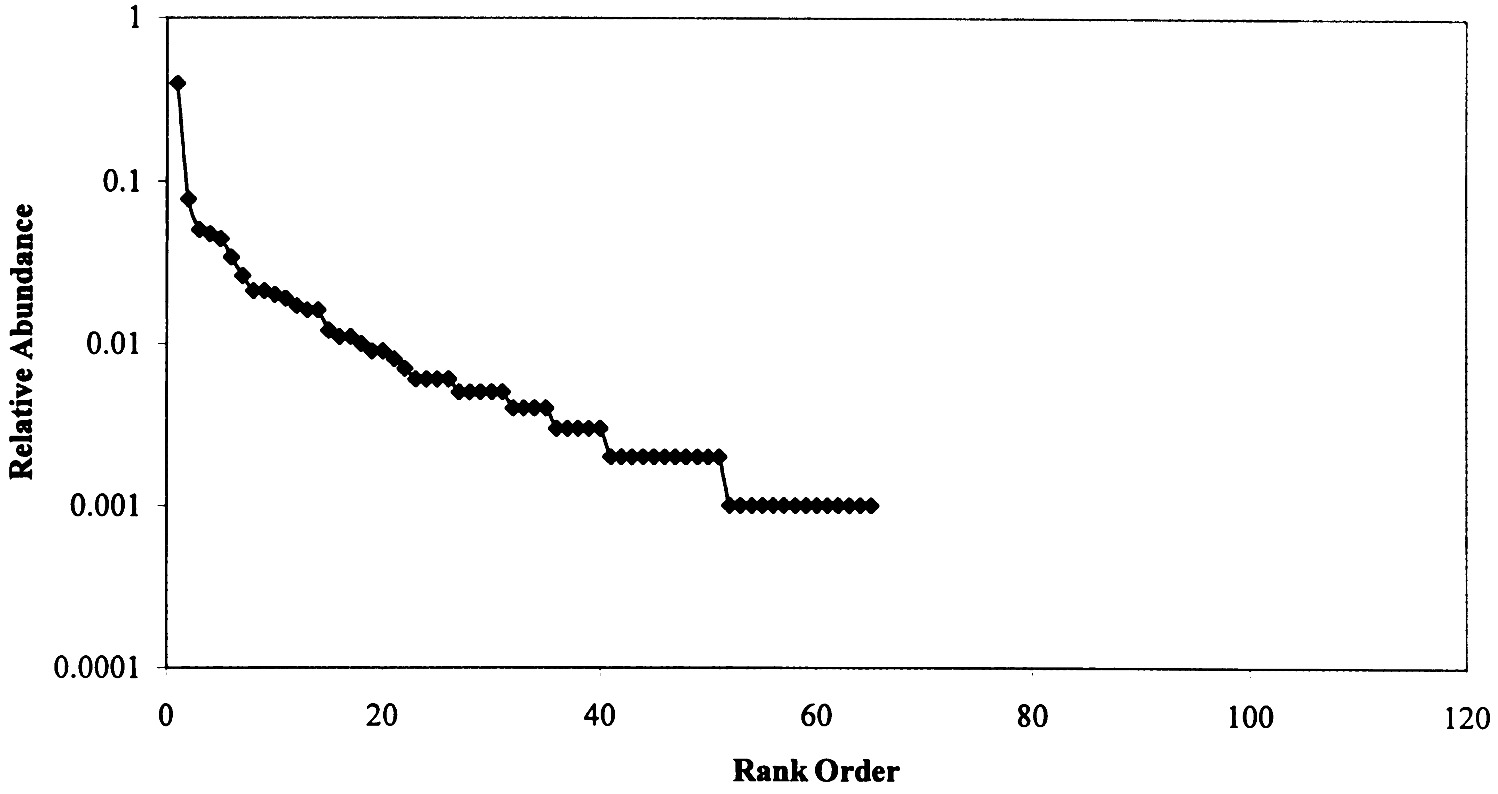


Figure B2.28: Dominance-diversity curve of Site 28, southwestern Puerto Rico

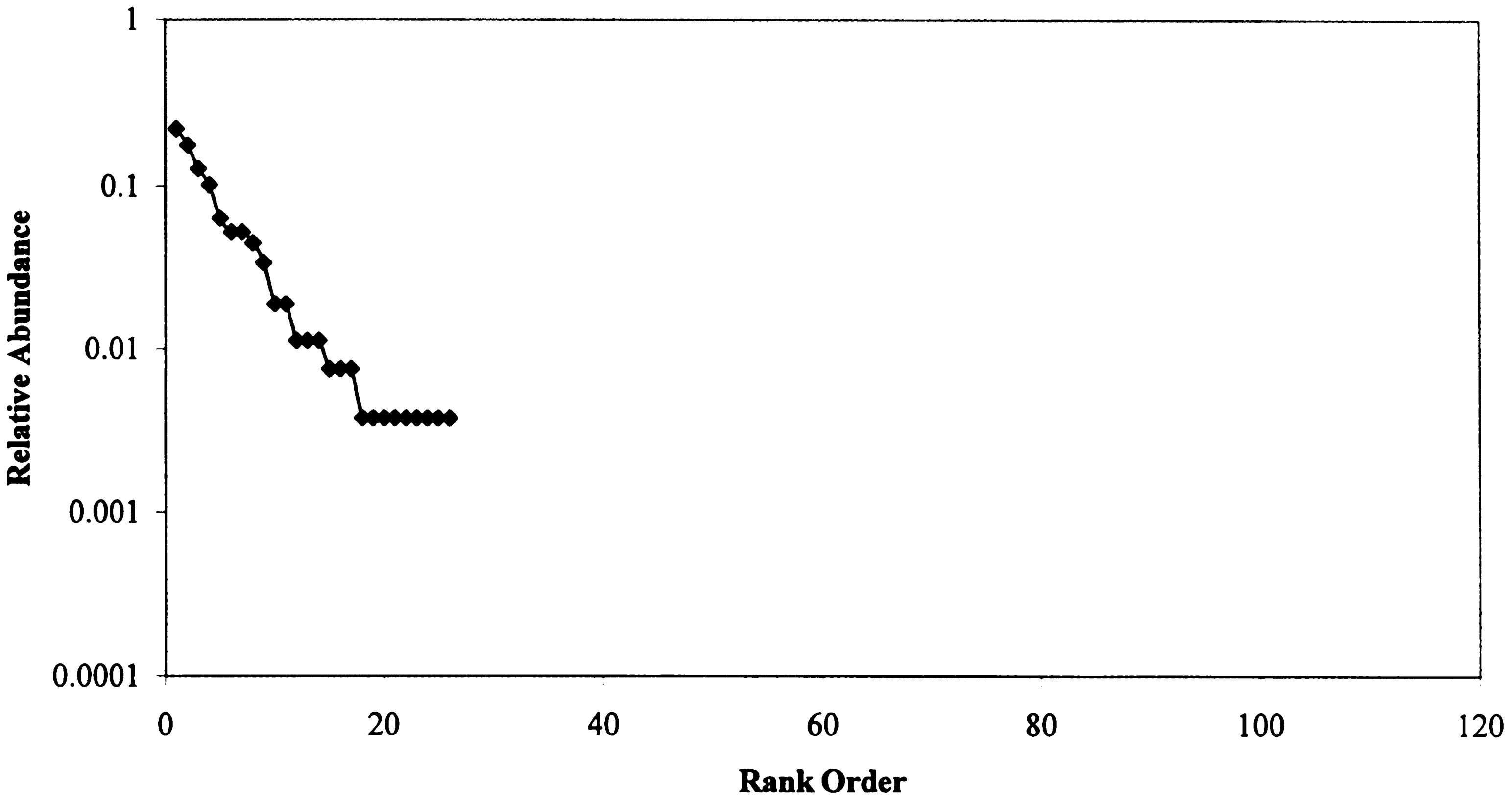


Figure B2.29: Dominance-diversity curve of Site 29, southwestern Puerto Rico

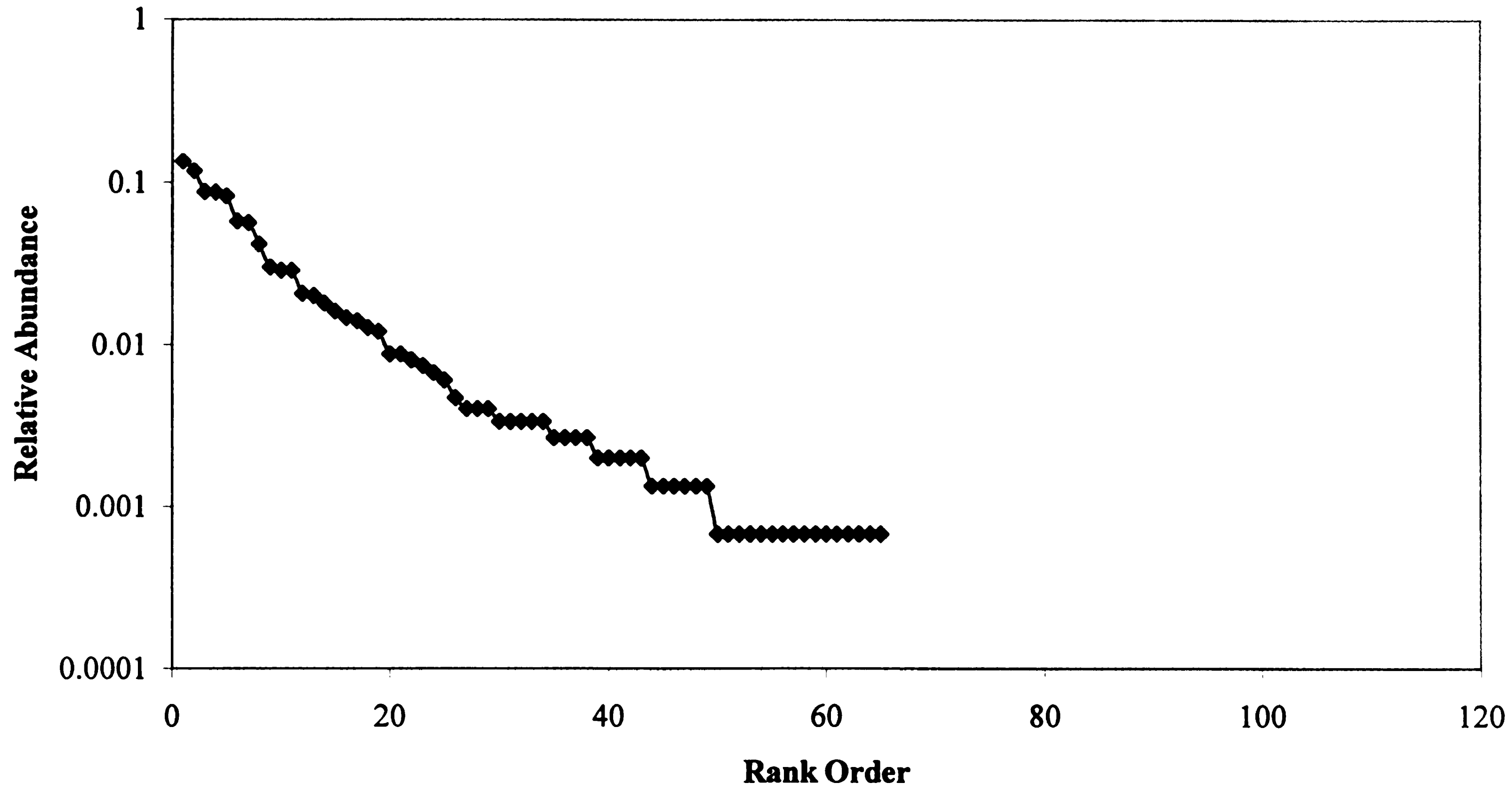


Figure B2.30: Dominance-diversity curve of Site 30, southwestern Puerto Rico

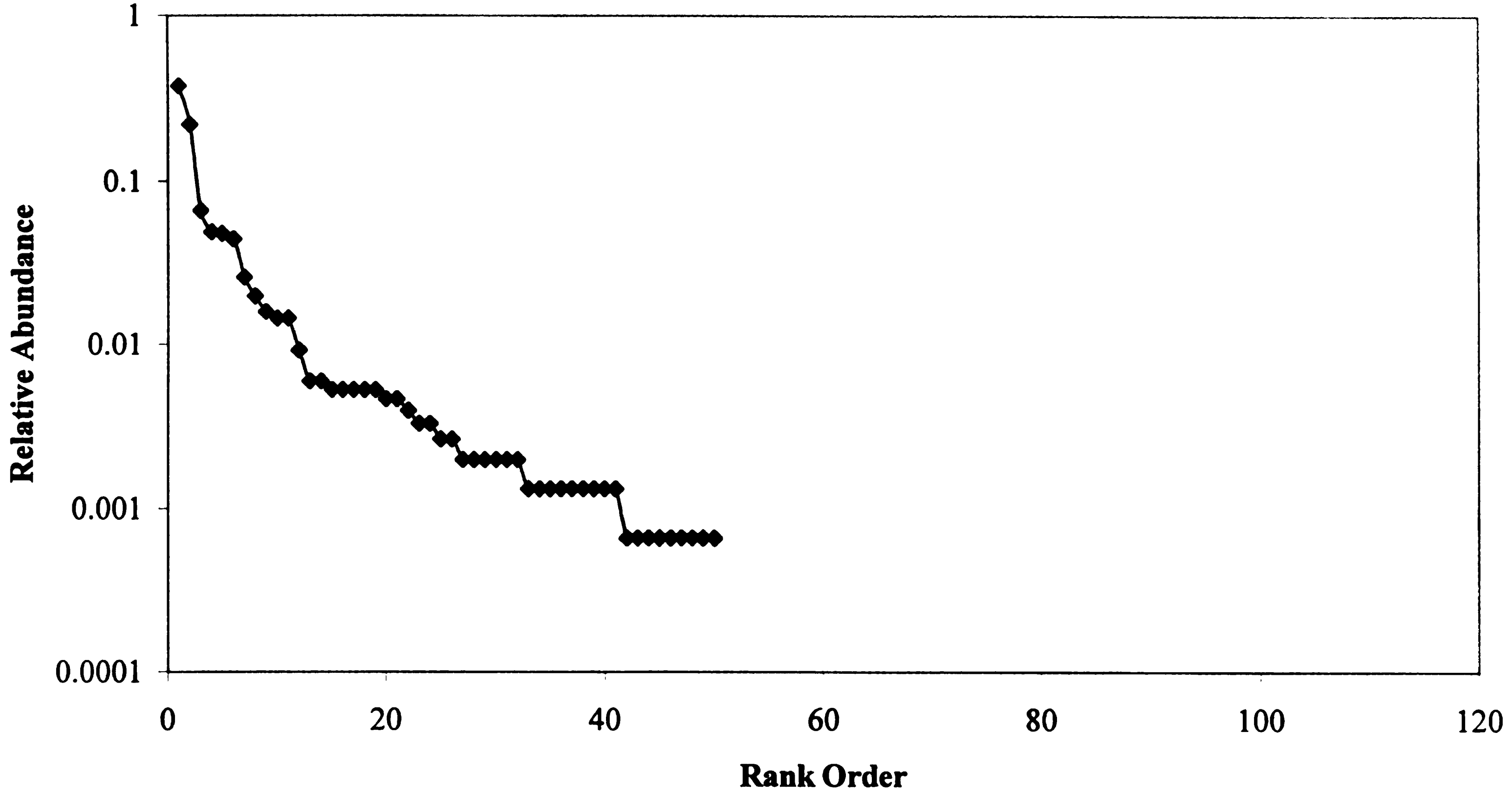


Figure B2.31: Dominance-diversity curve of Site 34, southwestern Puerto Rico

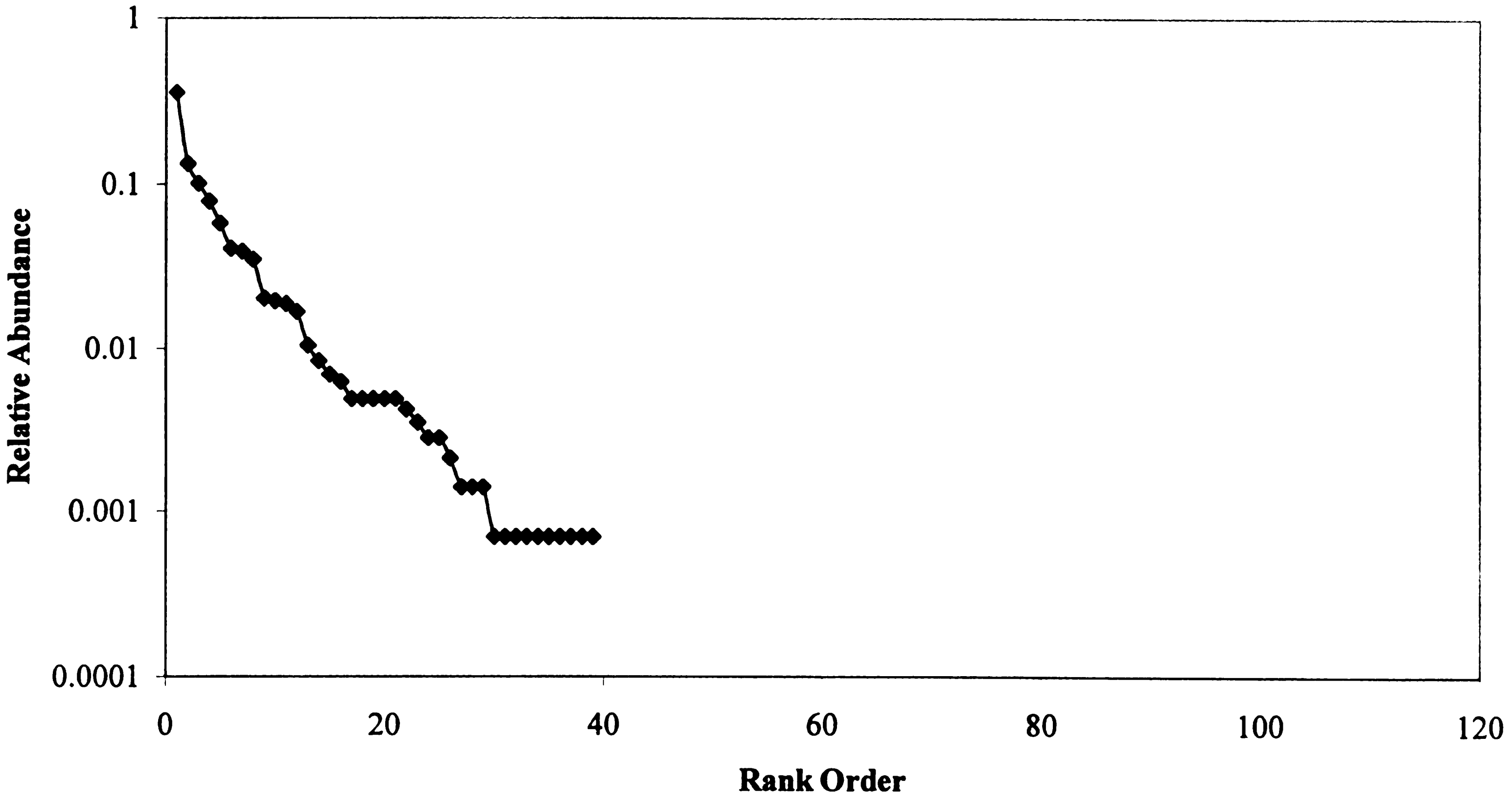


Figure B2.32: Dominance-diversity curve of Site 35, southwestern Puerto Rico

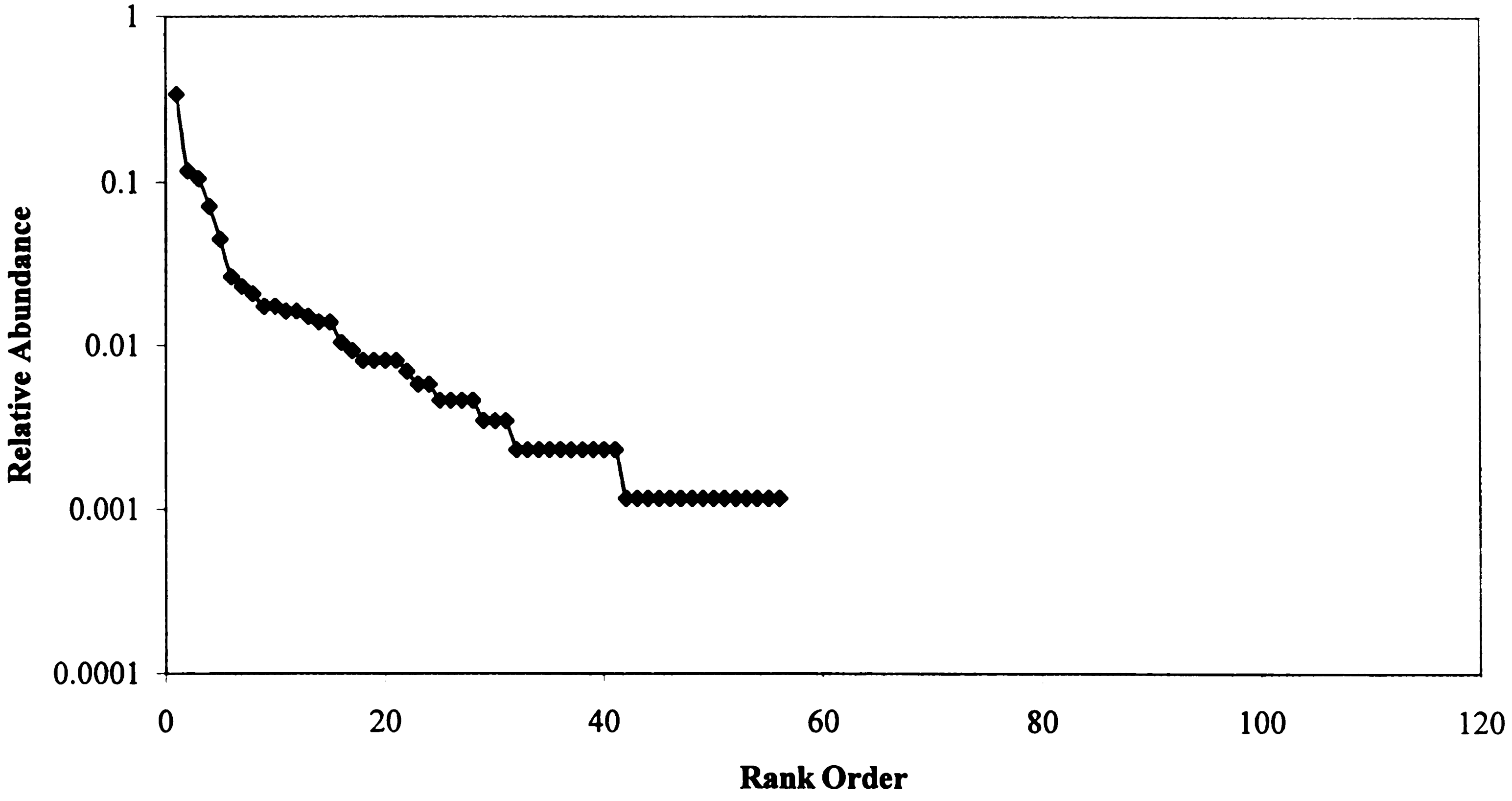


Figure B2.33: Dominance-diversity curve of Site 36, southwestern Puerto Rico

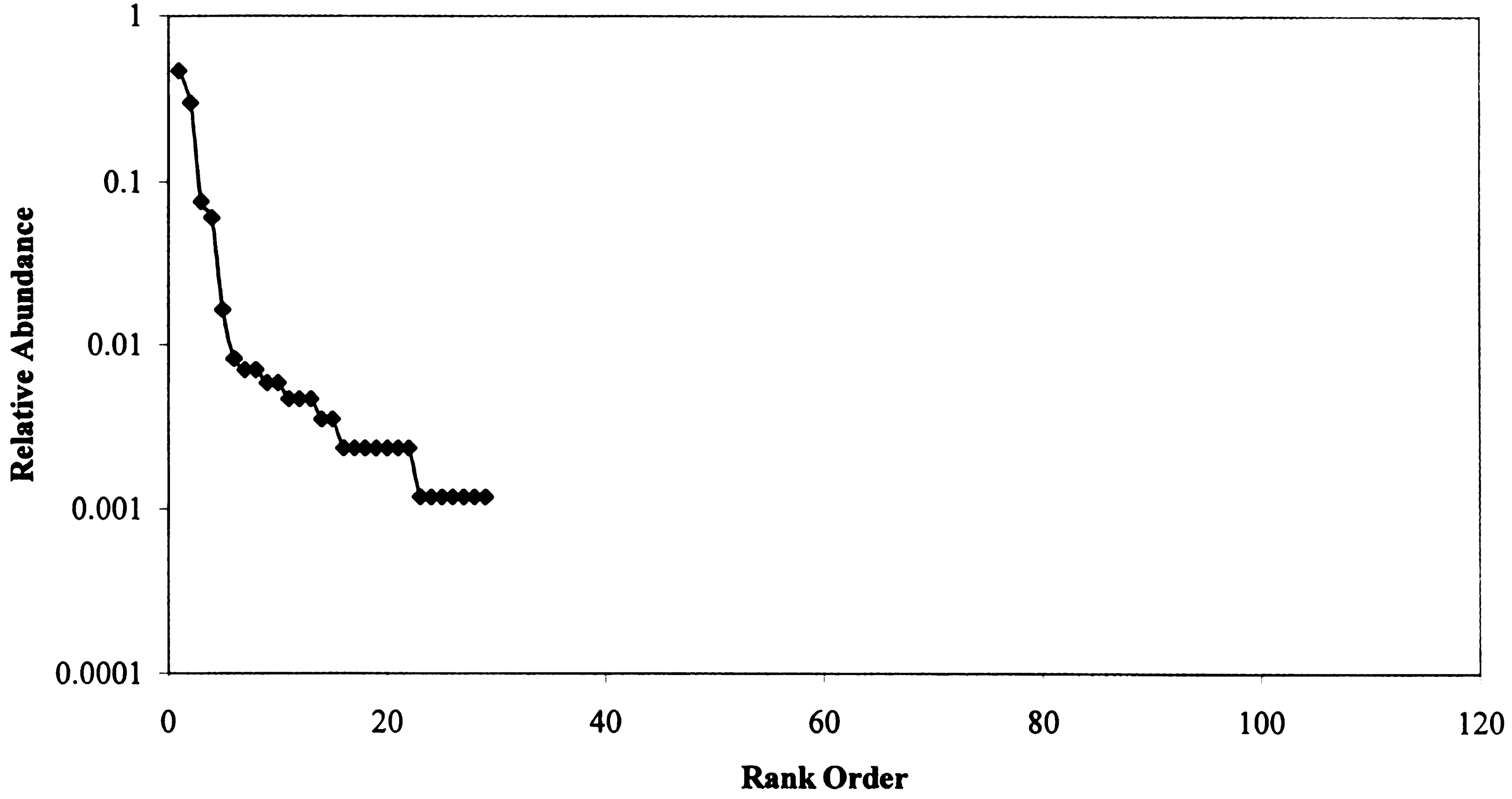


Figure B2.34: Dominance-diversity curve of Site 37, southwestern Puerto Rico

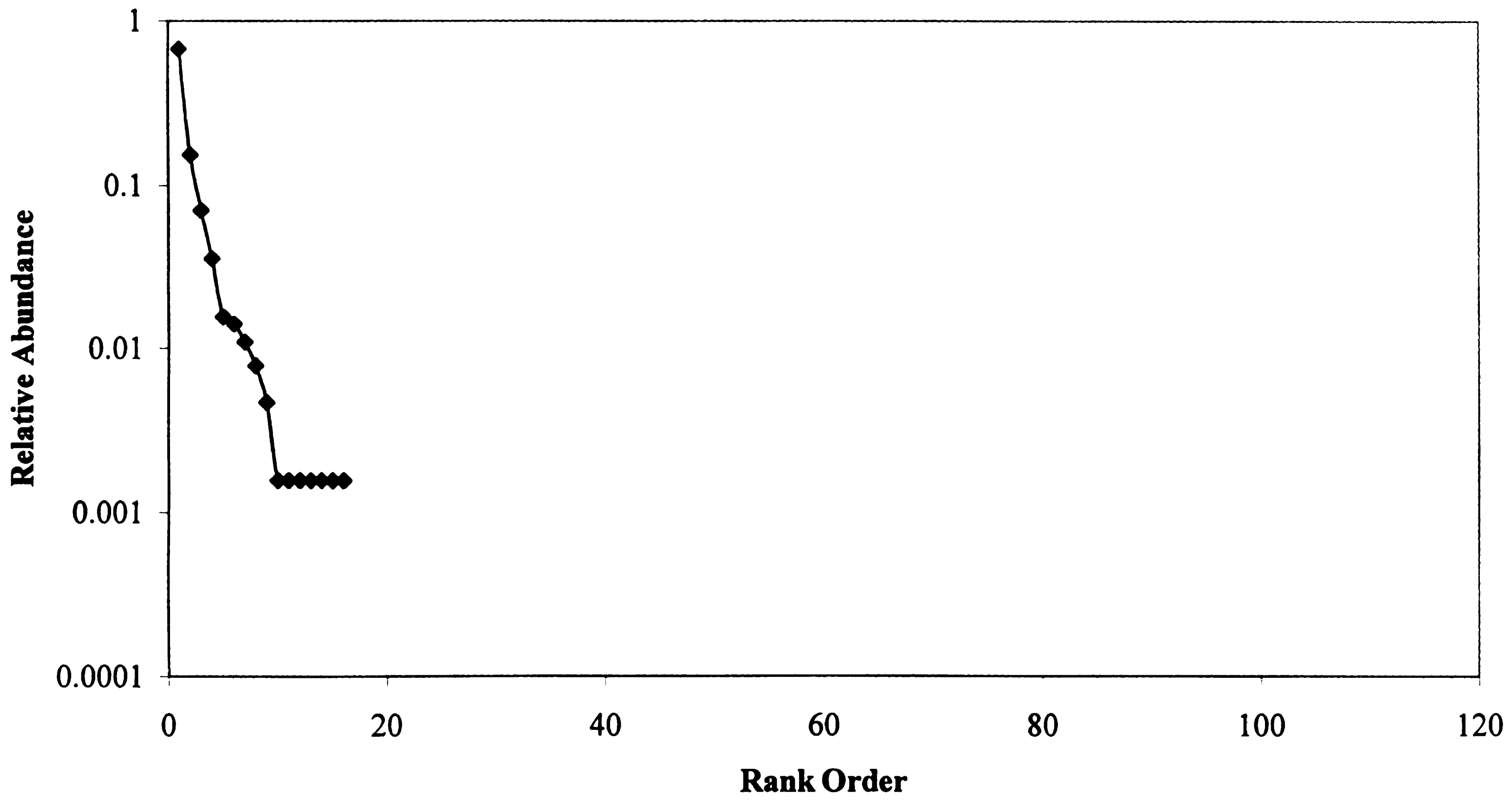


Figure B2.35: Dominance-diversity curve of Site 38, southwestern Puerto Rico

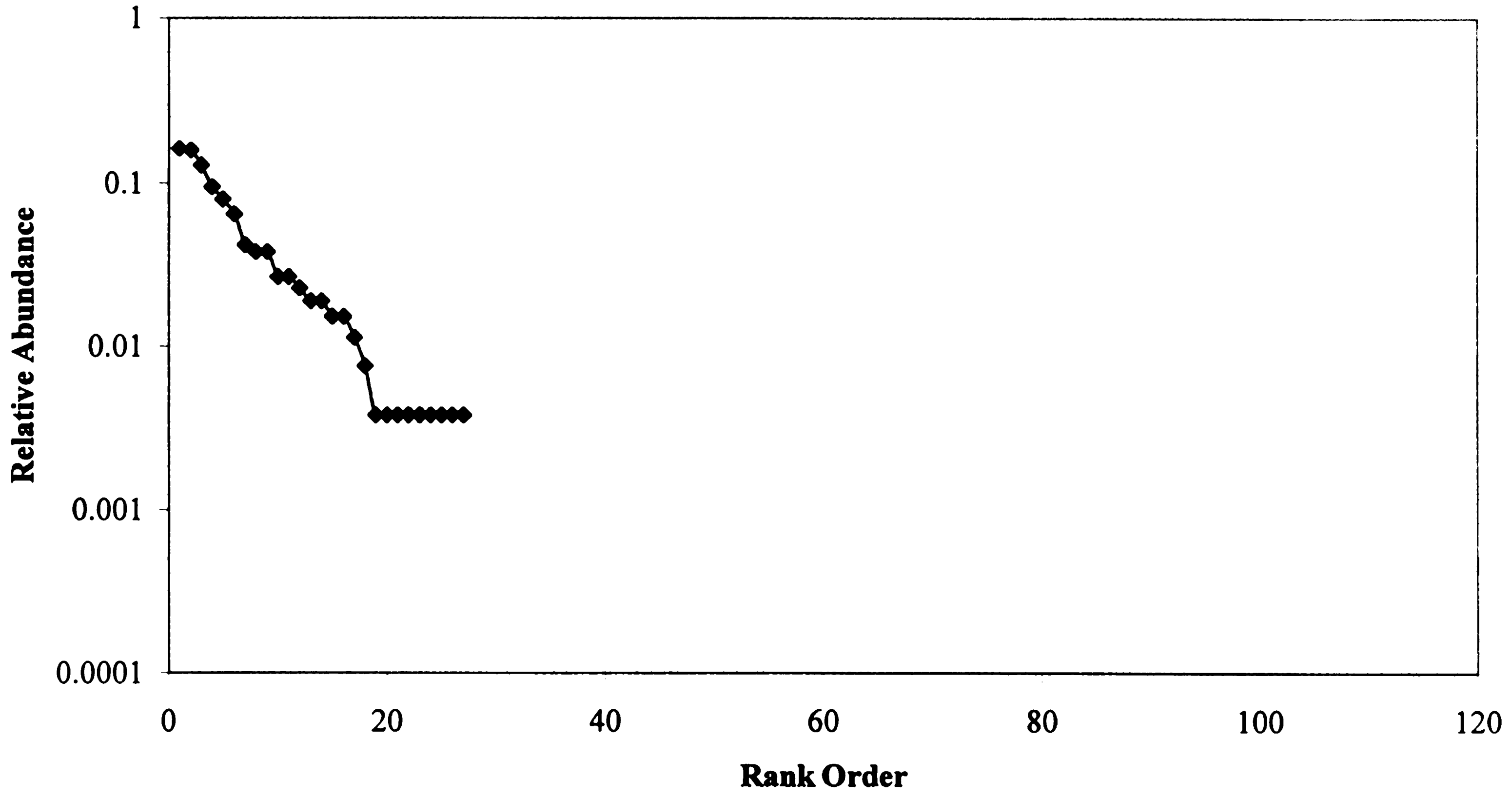


Figure B2.36: Dominance-diversity curve of Site 39, southwestern Puerto Rico

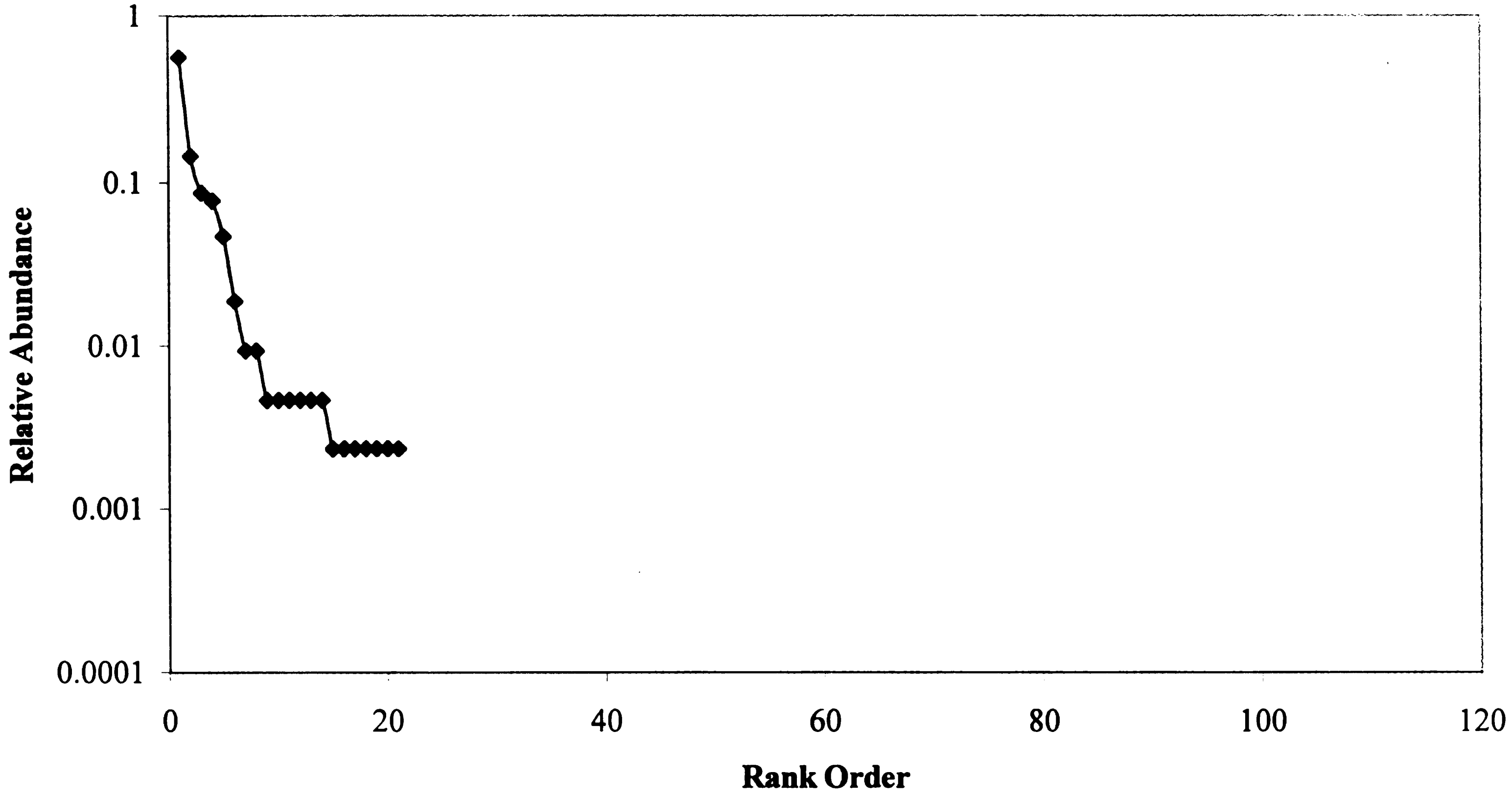


Figure B2.37: Dominance-diversity curve of Site 40, southwestern Puerto Rico

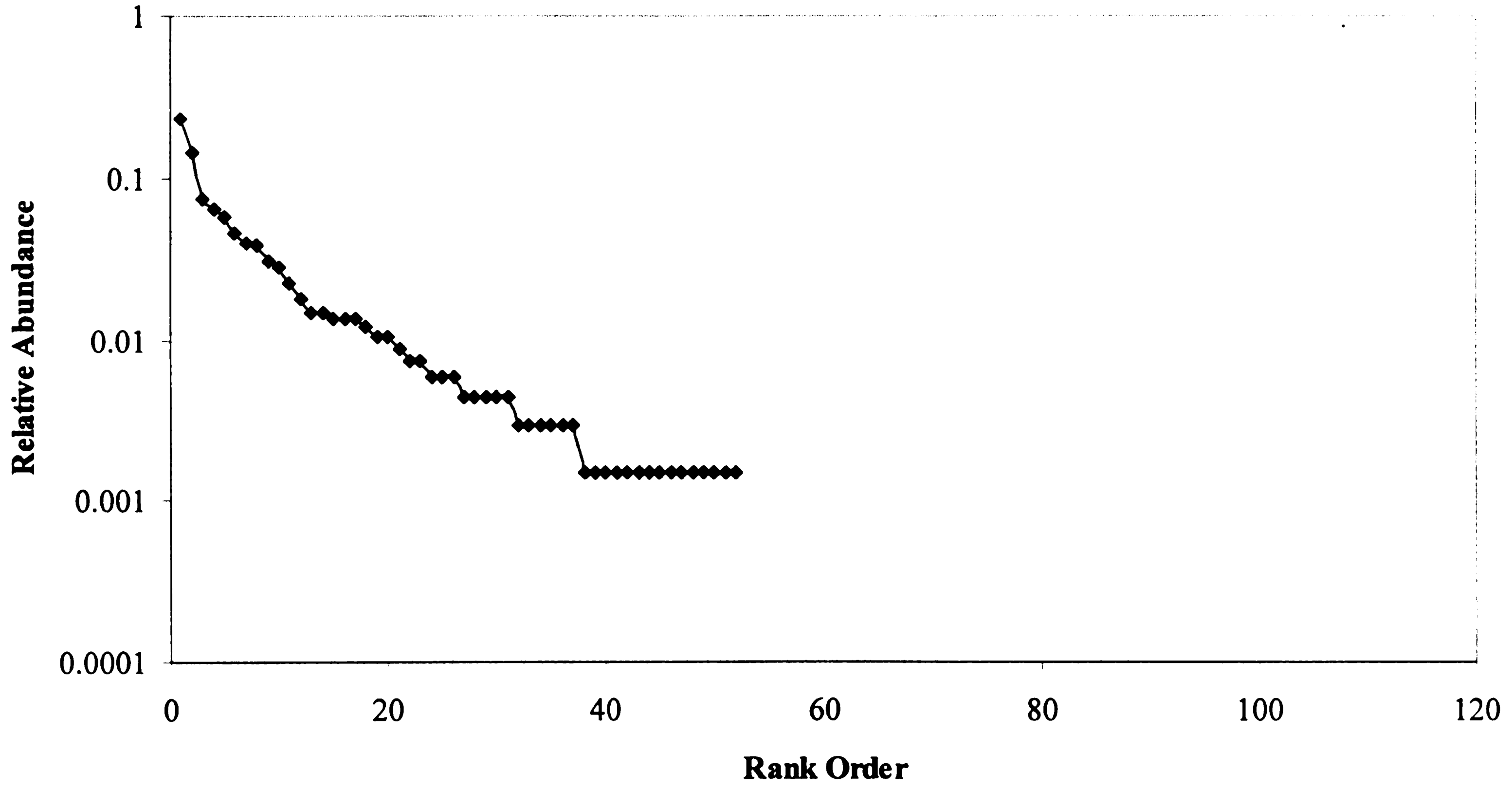


Figure B2.38: Dominance-diversity curve of Site 41, southwestern Puerto Rico

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