
Roads as Ecological Edges for Rehabilitating Coastal Dune Assemblages in Northern KwaZulu-Natal, South Africa

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Abstract

Post-mining coastal dune rehabilitation north of Richards Bay, KwaZulu-Natal started 20 years before field work for the present study commenced. This resulted in the development of a known age sere of coastal dune forest succession. These rehabilitating areas are fragmented by roads that may act as ecological edges. To establish whether roads affect regenerating bird, millipede, and rodent assemblages, multivariate techniques were applied to test for existence of edge and core assemblages within seral stages representative of the coastal dune forest successional sere. Edge and core assemblages were identified for both the bird and millipede communities but not for the rodent community. Low rodent numbers may have concealed edge effects, but the absence of edge and core assemblages

could also be ascribed to the absence of a forest core. In the bird community species composition, richness, density, and total number of species contributed to the identification of edge and core assemblages. Within seral stages the species composition of millipedes differed between the edge and core assemblages. However, if the site was the same age the number of species in edge and core assemblages was similar. The generality of the edge concept should be approached with caution when dealing with taxa comprising species with such diverse natural histories as in the present study. It should also be kept in mind that some species require forest interiors for survival.

Key words: birds, edge effects, millipedes, mining, rehabilitation, roads, rodents.

Introduction

During the last decade large-scale tropical deforestation has led to fragmentation of continuous forests, leaving only islands of natural habitat (Feinsinger 1994) with small functional interior areas (Fraver 1994). Through secondary succession, recolonization of deforested land offers hope that some of the unique characteristics of ecosystems may be restored (Finegan 1996). However, despite restoring species richness, species compositions of restored areas may differ markedly from that of mature forests on comparable sites (Finegan 1996). This may be due partially to the influence of edge effects on the recovering ecosystem (Turner & Corlett 1996).

In ecological terms the core of a forest is the center that remains unaffected after fragmentation (Restrepo & Gómez 1998). An edge is defined as a zone where two plant communities meet, where successional stages within plant communities come together (Noss 1983), or a division within a habitat type. Abutting communities may influence each other, especially on the boundary. Here, increased light penetration may change vegetation composition (Fox et

al. 1997), whereas an increase in weed and pioneer species at the edge (Oliviera-Filho et al. 1997) may result in an increase in total species richness but a decrease in forest species richness (Saunders et al. 1991).

Our study area on the coast of KwaZulu-Natal, South Africa is the outcome of a post-mining rehabilitation program that started 20 years before the present study. This program gave rise to the development of a known age sere of coastal dune forest succession (van Aarde et al. 1996b). The differently aged sites vary in size and shape and are bordered either by unmined indigenous forest (forest dominated by species such as *Celtis africana* and *Trichilia emetica*; Table 1), commercial beefwood (*Casuarina equisetifolia*) plantations, mined sand dunes, or other regenerating dune forests. A network of service roads and tracks runs through the rehabilitating sites, dividing them into smaller fragments. The present study aims at determining the implications of roads passing through the rehabilitating forests, in relation to successional development. The edge influence was addressed by using multivariate techniques to determine whether edge and core assemblages can be distinguished for the bird, millipede, and rodent assemblages in different seral stages. These taxa were selected because recent studies have been undertaken on their development during dune rehabilitation in the study sites selected for the present study (Ferreira 1993; Kritzing 1996; van Aarde et al. 1996a). Furthermore, they represent different levels in the coastal dune food web and have different functions in the ecosystems.

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Table 1. A description of the vegetation in the rehabilitating and unmined sites in the study area.

Age of Site (yr)	Description
10	Rehabilitating area comprised of <i>Acacia karroo</i> (sweet thorn) woodland with canopy 8–10 m high. Other indigenous species such as <i>Brachylaena discolor</i> (coast silver oak) and <i>Vepris lanceolata</i> (white ironwood) occur at low densities. Ground cover is sparse and mainly dominated by <i>Digitaria diversinervis</i> (finger grass) and <i>Dactyloctenium geminatum</i> (L. M. grass).
14	<i>A. karroo</i> woodland with a 9–12 m high canopy of colonizing secondary dune forest tree species. These include <i>Trichilia emetica</i> (Natal mahogany), <i>Celtis africana</i> (white stinkwood), <i>V. lanceolata</i> , and <i>Kraussia floribunda</i> (rhino-coffee). The plant community is much denser than in the 10-year-old site. Ground cover is dominated by <i>D. diversinervis</i> and is not as extensive as in the 18-year-old site.
18	Rehabilitating area still dominated by <i>A. karroo</i> (canopy 10–14 m high), colonized by a variety of secondary dune forest species. These secondary dune forest species include <i>Mimusops caffra</i> (coastal red milkwood), <i>C. africana</i> , <i>Albizia adianthifolia</i> (flat-crown), <i>T. emetica</i> , <i>K. floribunda</i> , and <i>Trema orientalis</i> (pigeon wood). Climbers include <i>Sarcostemma viminalis</i> (caustic creeper) and <i>Adenia gummifera</i> (umphindamshaya) with <i>Asystasia gangetica</i> (isiaobo) as one of the common ground cover species.
Unknown (unmined forest)	Unmined area comprised of a secondary coastal dune forest with a canopy of 12–15 m or higher. Several vertical strata are present with a high diversity of species in each strata. Canopy species include <i>C. africana</i> , <i>T. emetica</i> , and <i>A. adianthifolia</i> . The middle stratum consists of species such as <i>Ochna natalitia</i> (Mickey Mouse bush), <i>Tricalysia sonderiana</i> (coast coffee), and <i>Carissa bispinosa</i> (forest num-num). <i>Issoglossa woodii</i> (herb) occurs frequently on the forest floor.

Adapted from van Aarde et al. (1996b) and Ferreira (1997).

Methods

North of Richards Bay (28°43'S, 32°12'E) sand dunes are presently being mined by the company Richards Bay Minerals. After mining a third of the area is rehabilitated to indigenous vegetation (see Table 1 for characteristic species associated with indigenous areas), whereas the remaining two-thirds of the area is revegetated with exotic beefwood for the development of a local charcoal industry (van Aarde et al. 1996b).

Sampling took place on indigenous rehabilitating sites 10, 14, and 18 years old and an unmined relatively undisturbed area of unknown age. All these sites are fragmented by roads cutting through them. In each study site five clusters of sampling lines, each consisting of five transect lines, were placed perpendicular to the road. Transect line clusters were situated 10 meters apart and the clusters within a site were at least 50 meters apart. Due to variation in width of the sites, lines ranged from 80 to 210 meters in length. A brief description of vegetation variables for each of these sites is presented in Table 1. A detailed description of the study site and dune rehabilitation processes as well as site photographs have been published by van Aarde et al. (1996b).

Rodents were trapped between 13 January and 5 March 1998 along all transect lines. During a trapping session all lines were sampled for 5 consecutive days and nights. Sherman live-traps (7.5 × 9 × 23 cm) were set singly at 10-meter intervals along the entire distance of the transect lines. Traps were baited with oats, peanut butter, and raisins. Individuals captured were identified to species level and marked (by toe-clipping) before being released. In the

10-year-old site too few individuals were caught for meaningful analysis. This site was therefore excluded from further analyses of rodent data. Distance-specific relative densities for each study site are expressed as means and standard errors of means of the frequencies of captures per trap for each distance in every cluster (Caughley 1977).

Transects were surveyed in a random order for the presence of birds on nonrainy and nonwindy days between 22 August and 24 October 1997. Sampling started at dawn and ended at 1100 hr. Sampling consisted of 12-minute time periods spent (at a fixed location) at 10-meter intervals along each of the transect lines. To allow the birds to become accustomed to the observer's presence, no observations were recorded during the first 2 minutes at a sampling point. Birds flying, except when they were seen to land in the area, were excluded. Birds were recorded only if seen. To establish the distance of the bird from the observer, an imaginary line was drawn from where the bird was first observed to the ground. This distance from the observer to the spot on the ground was calculated using a "ranging" range finder (Telinject Ranging TLR 75, Telinject, USA Inc., Saugus, CA) calibrated at 0.5-meter intervals from 9 to 13 meters and at 1-meter intervals from 13 to 40 meters. Each observation was placed in one of the distance classes (e.g., 0–9 meters, 10–19 meters, etc.) from the observation point. The total number of individuals of each species within a distance class on each of the transect clusters provided an abundance value for that cluster. The associated measures of variance were recorded for each site. We assumed that all birds present were seen, that birds were recorded at their initial distance from the edge, and that all distance estimates were accurate.

The millipede surveys were based on quadrats (3×15 meters) placed at the edge (0 meters), 20, 40, 60, 80, 100, and 120 meters along transect lines set out randomly throughout the site (the longest side of the quadrant parallel to the edge). Sampling of millipedes consisted of searching through litter and shrub strata and observing the tree strata for millipedes. Sampling was conducted from 28 October to 28 November 1997 from dawn to 1100 hr, this representing the peak period of millipede activity (van Aarde et al. 1996a). Sampling of transects continued until the coefficient of variation of density estimates reached a plateau. These values leveled off at 13, 12, 19, and 14 transect lines set out in the 10-, 14-, 18-year-old and unmined sites, respectively. Distance-specific densities were calculated as number of individuals per square meter and are presented as mean values for each species, followed by a standard error of the mean for each of the distance classes.

Nonmetric multidimensional scaling (MDS) (computer software package PRIMER, Plymouth Routines in Multivariate Ecological Research, Plymouth Marine Laboratory, UK) was used to determine whether edge and core assemblages existed for each taxon on each sampling site. Data were arranged as a matrix for each community variable (a value for each species) and distance from edge. Fourth-root transformation was applied to all data to down-weight the effect of abundant species and to enable less dominant and rare species to contribute significantly to the analyses. This transformation ensures the most biologically sensible interpretation of MDS results (Clarke & Warwick 1994). The similarity matrix was calculated using the nonmetric Bray-Curtis similarity coefficient. Calculated stress values indicated the distortion between the similarity rankings and the corresponding distance rankings in the ordination plot of the MDS (Clarke & Warwick 1994). Species richness (mean number of species per sampling distance), species diversity (Shannon Wiener's diversity index), total number of individuals, total number of species, and species composition were calculated for each taxon within each edge and core assemblage. Analysis of similarity was used to test for significant differences between these assemblages (PRIMER) and whether replicates from different sites varied more than replicates

within sites. The highest similarity corresponds to an R value of 1 (Clarke & Warwick 1994).

If edge and core assemblages occurred, SIMPER analysis (PRIMER), which computes the dissimilarity among all pairs of edge and core assemblages by comparing every species in the edge assemblage with every species in the core assemblage, was conducted. Species contributing most to differences between edge and core were identified as discriminant species and species contributing most to similarity within edge and core as typical edge or core species.

Results

For rodents no distinction could be made between edge and core assemblages (Table 2). However, such assemblages were identified for birds in all four study sites (Table 2). For birds species richness and diversity at the edge decreased with an increase in habitat regeneration age but increased with age in the core assemblage (Table 3). The 14-year-old site did not follow this trend. The number of individuals increased in edge and core assemblages with increasing site regeneration age, but the lowest number of individuals was recorded in the edge assemblage of the unmined site (Table 3). The total number of species in edge assemblages of regenerating sites also was higher than in the edge assemblage of the unmined forest. However, core assemblages of the regenerating sites had more species than that of the unmined forest (Table 3). R values (ANOSIM, measure of the degree of separation between study sites) for all seral stages were significant (10-year-old site, $R = 0.97$, $p < 0.0001$; 14-year-old site, $R = 0.933$, $p < 0.0001$; 18-year-old site, $R = 0.987$, $p = 0.001$; unmined forest, $R = 0.601$, $p = 0.007$). The discriminant species of the edge and core assemblages differed for all study sites, but typical species were the same for the edge and core assemblages of regenerating sites (Table 3).

The MDS analyses distinguished between edge and core millipede assemblages for all study sites (Table 2). The width of edge assemblages increased from the 14-year-old site to the unmined forest (Table 2). Species richness increased with an increase in regeneration age in the core assemblage but not edge assemblage (Table 4). Millipede species diversity for core assemblages increased with in-

Table 2. Distance measures in meters for edge and core assemblages as suggested by MDS.

Taxon	Study Site											
	10-Year-Old Rehabilitating Site			14-Year-Old Rehabilitating Site			18-Year-Old Rehabilitating Site			Unmined Forest of Unknown Age		
	Edge	Core	Stress	Edge	Core	Stress	Edge	Core	Stress	Edge	Core	Stress
Birds	5–105	115–125	0.08	5–55	65–195	0.12	5–115	125–175	0.15	5–25	35–125	0.13
Millipedes	10 & 20	0 & 40–80	0.01	0–10	20–100	<0.0001	0–20	40–120	<0.0001	0–40	60–80	0.04
Rodents	None	None	—	—	—	0.05	—	—	0.01	—	—	0.01

The distinction between edge and core assemblages results from differences in species composition, species richness, species diversity, and number of individuals measured as Bray-Curtis distances by the program PRIMER (Clarke & Warwick 1994). A stress value < 0.05 suggests an excellent representation, stress values < 0.1 correspond to a good ordination with no misleading interpretations, and stress values < 0.2 indicate an interpretation still useful, though the values at the upper end of the range should not be considered with too much reliance (Clarke & Warwick 1994).

Table 3. The mean (\pm standard error) species richness, species diversity, and number of individuals for edge and core assemblages.

Community Variables	Study site								
	10-Year-Old Rehabilitating Site		14-Year-Old Rehabilitating Site		18-Year-Old Rehabilitating Site		Unmined Forest of Unknown Age		
	Edge	Core	Edge	Core	Edge	Core	Edge	Core	
Species richness	12.3 \pm 1.4	3.8 \pm 0.8	8.2 \pm 1.0	3.5 \pm 0.4	11.7 \pm 1.0	5.3 \pm 1.4	7.7 \pm 0.3	7.2 \pm 1.1	
Shannon diversity	2.0 \pm 0.09	1.0 \pm 0.1	1.7 \pm 0.1	0.9 \pm 0.1	2.0 \pm 0.09	1.5 \pm 0.2	1.7 \pm 0.5	1.7 \pm 0.2	
Number of individuals	4.7 \pm 0.7	1.9 \pm 0.7	4.8 \pm 1.1	2.5 \pm 0.3	11.7 \pm 1.5	6.8 \pm 1.1	2.8 \pm 0.5	2.5 \pm 1.3	
Total number of species	31	11	23	19	31	15	17	28	
Species composition	Black-eyed Bulbul* Blue-grey Flycatcher* Black Sunbird* Bleating Warbler Collared Sunbird	Bleating Warbler Cape White-eye Forest Weaver Fork-tailed Drongo* Golden-rumped Tinker Barbet	African Goshawk Black-eyed Bulbul Blue-grey Flycatcher* Bleating Warbler Collared Sunbird*	Black-eyed Bulbul Bleating Warbler Blue-grey Flycatcher Cape White-eye Fork-tailed Drongo*	Black Cuckooshrike* Blue-grey Flycatcher Bleating Warbler Collared Sunbird Cape White-eye	African Scops Owl Bearded Woodpecker Black-bellied Starling* Black Cuckooshrike Black-eyed Bulbul	Black Cuckooshrike* Blue-grey Flycatcher Bleating Warbler Collared Sunbird Cape White-eye	Bleating Warbler Black-eyed Bulbul Collared Sunbird Dusky Flycatcher* European Cuckoo	Black-bellied Starling* Blue-grey Flycatcher* Black Sunbird Black-eyed Bulbul Bleating Warbler
	Cape White-eye European Cuckoo* Fork-tailed Drongo	Olive Sunbird Puffback	Cape White-eye Dusky Flycatcher* Forest Weaver	Forest Weaver Olive Sunbird Puffback	Blue-grey Flycatcher Bleating Warbler Cape White-eye	Forest Weaver Golden-rumped Tinker Barbet* Natal Robin	Forest Weaver Fork-tailed Drongo Natal Robin	Cape White-eye* Collared Sunbird Crowned Hornbill	
	Fan-tailed Flycatcher* Forest Weaver* Golden-rumped Tinker Barbet Grey Sunbird	Spotted-backed Weaver White-browed Robin* White-bellied Sunbird Yellow-breasted Apalis	Golden-rumped Tinker Barbet* Livingstone Lourie Natal Robin* Olive Sunbird Puffback	Paradise Flycatcher Pygmy Kingfisher* Sombre Bulbul* Square-tailed Drongo Masked Weaver*	Paradise Flycatcher Cuckoo Hawk Dusky Flycatcher Fork-tailed Drongo Fork-tailed Drongo Masked Weaver*	Olive Sunbird Puffback Square-tailed Drongo Tawny-flanked Prima White-bellied Sunbird*	Olive Sunbird Puffback Square-tailed Drongo Spotted Flycatcher Scarlet-chested Sunbird	Dusky Flycatcher Fork-tailed Drongo Forest Weaver Golden-rumped Tinker Barbet Little Bee-eater	
	Long-billed Crombec Natal Robin Olive Sunbird	White-bellied Sunbird Yellow-breasted Apalis	Livingstone Lourie Natal Robin* Olive Sunbird Puffback	Pygmy Kingfisher* Sombre Bulbul* Square-tailed Drongo Masked Weaver*	Dusky Flycatcher Cuckoo Hawk Dusky Flycatcher Fork-tailed Drongo Fork-tailed Drongo Green Twinspot	Golden-rumped Tinker Barbet Yellow-breasted Apalis Yellow-bellied Bulbul	Puffback Sombre Bulbul Spotted Flycatcher Scarlet-chested Sunbird Tambourine Dove	Fork-tailed Drongo Forest Weaver Golden-rumped Tinker Barbet Little Bee-eater Long-crested Eagle	
	Paradise Flycatcher Puffback	White-bellied Sunbird Yellow-breasted Apalis	Rattling Cisticola Red-eyed Dove Square-tailed Drongo	White-bellied Sunbird Yellow-breasted Apalis Yellow Weaver*	Lizard Buzzard Natal Robin Olive Sunbird Puffback	White-eared Bulbul Yellow-bellied Bulbul Yellow-eyed Canary	White-eared Bulbul Yellow-bellied Bulbul Yellow-eyed Canary	Natal Robin Olive Sunbird Puffback Sombre Bulbul	
	Pygmy Kingfisher* Rudd's Apalis*	White-bellied Sunbird Square-tailed Drongo Masked Weaver*	Tambourine Dove Tawny-flanked Prima White-bellied Sunbird Yellow-breasted Apalis Yellow-eyed Canary*	Yellow-bellied Bulbul Yellow Weaver*	Paradise Flycatcher Sombre Bulbul Scarlet-chested Sunbird Square-tailed Drongo Spotted Flycatcher Terrestrial Bulbul Tambourine Dove Tawny-flanked Prima White-tailed Flycatcher Yellow-breasted Apalis Yellow-bellied Bulbul Yellow-eyed Canary	Paradise Flycatcher Sombre Bulbul Scarlet-chested Sunbird Square-tailed Drongo	Southern Boubou* Square-tailed Drongo* Thick-billed Weaver White-browed Robin		
	Sombre Bulbul* Square-tailed Drongo Masked Weaver*	White-bellied Sunbird Yellow-bellied Bulbul Masked Weaver*	White-bellied Sunbird Yellow-bellied Bulbul Yellow-breasted Apalis Yellow-eyed Canary*	Yellow-bellied Bulbul Yellow Weaver*	Paradise Flycatcher Sombre Bulbul Scarlet-chested Sunbird Square-tailed Drongo	Paradise Flycatcher Sombre Bulbul Scarlet-chested Sunbird Square-tailed Drongo	Southern Boubou* Square-tailed Drongo* Thick-billed Weaver White-browed Robin		
	Spotted-backed Weaver Tambourine Dove* Tawny-flanked Prima* White-browed Robin White-bellied Sunbird Yellow Weaver* Yellow-breasted Apalis Yellow-bellied Bulbul Yellow-spotted Nicator*	White-bellied Sunbird Yellow-breasted Apalis Yellow-eyed Canary*	White-bellied Sunbird Yellow-bellied Bulbul Yellow-breasted Apalis Yellow-eyed Canary*	Yellow-bellied Bulbul Yellow Weaver*	Paradise Flycatcher Sombre Bulbul Scarlet-chested Sunbird Square-tailed Drongo	Paradise Flycatcher Sombre Bulbul Scarlet-chested Sunbird Square-tailed Drongo	Southern Boubou* Square-tailed Drongo* Thick-billed Weaver White-browed Robin		
								White-eared Bulbul* Yellow-breasted Apalis* Yellow-bellied Bulbul* Yellow-eyed Canary Yellow Weaver	

The species compositions of the edge and core assemblages are listed. The core and edge assemblages were identified as described and indicated in Table 2. The discriminant species (indicated by an asterisk) and typical species (indicated by underlining) are shown. In all cases, $n = 5$.

creasing regeneration age, but number of millipede individuals in edge and core assemblages varied with increasing regeneration age (Table 4). The unmined forests had higher total numbers of millipede species than any of the assemblages in the rehabilitating areas (Table 4). Analysis of similarity showed significant differences between these assemblages in the 10-year-old site ($R = 0.75, p = 0.067$), 14-year-old site ($R = 1.00, p = 0.048$), 18-year-old site ($R = 0.92, p = 0.018$), and unmined forest ($R = 0.61, p = 0.051$). Typical and discriminant species were identified for all the study sites (Table 4).

Discussion

The most important finding of the present study is that roads exert an edge effect, causing a distinction between edge and core assemblages in the bird and millipede communities but not in the rodent community. Distance from the edge might affect species richness, diversity, and number of individuals and therefore the separation of sites into distinct edge and core assemblages.

Rodents occurred at very low densities in the study sites, resulting in distance-related trends and the impact of edges being concealed. It has been argued, however, that edges function as refugia for small mammals during food scarcity due to a higher diversity and richness of vegetation at edges in older areas (Hansson 1998). The absence of any identifiable edge and core assemblages for the rodent community in any of the study sites suggests that the effect of the current level of fragmentation may be too extensive, resulting in the absence of an identifiable forest core for rodents. Our inability to distinguish edge and core assemblages among rodents may also be due to these animals not being sensitive to differences in edge and core habitats. Here differences between edge and core may not be enough to influence population densities of rodents at edges (see Heske 1995; Swihart & Slade 1984). The low densities at which rodents occurred may also disguise the edge effects.

In a newly fragmented area edge species may be expected to replace core species (see Gates & Giffen 1991). In our study bird species associated with edges, such as the Black-eyed Bulbul (*Pycnonotus barbatus*), Blue-grey Flycatcher (*Muscicapa caerulescens*), and Collared Sunbird (*Anthreptes collaris*), usually occur in mixed habitat types or forage in the undergrowth (Maclean 1993). Such species are adapted to changing conditions prevailing on edges (also see Gates & Gysel 1978) and between neighboring habitats at edges (Andr n 1994).

Species such as the Yellow-eyed Canary (*Serinus mozambicus*) only occurred in the edge assemblages of the rehabilitating sites, but in both edge and core assemblages in the unmined forest. This species prefers thicker and more heterogeneous vegetation, such as that of the rehabilitating edges and throughout the unmined forest (Kritzing 1996). On the other hand, Bleating Warblers (*Camaroptera brachyura*) and Yellow-breasted Apalis (*Apalis flavida*)

were identified as typical species in both the edge and core assemblages in all rehabilitating sites. These species are common residents of thickets and forest edges (Maclean 1993). The identification of the Sombre Bulbul (*Andropadus importunus*) as a typical species for both edge and core assemblages of the unmined forest may be ascribed to its preference for dense foliage (Maclean 1993).

For millipedes the variable pattern in the 10-year-old site, where distance groups placed into either edge or core assemblages independent of distances from the edge, could be explained by the relatively homogeneous vegetation in this site. In the 10-, 14-, and 18-year-old rehabilitating site edges are maintained by cutting vegetation along the sides of the roads, thereby allowing vehicles passage of roads. A changing vegetation structure at the edge may "seal" the edge with more leaves and vegetation to transpire, while protecting the understory just inside the edge from desiccation (Camargo & Kapos 1995). The cutting of vegetation along the sides of the road, as well as the influence of the continuing changes due to secondary succession causing gaps, may explain the larger distance edge assemblages of the unmined forest than the rehabilitating sites. Although the species composition differed between edge and core assemblages within the same aged study site, the number of species contributing to these assemblages was quite similar throughout all study sites. In the present study some millipede species (e.g., *Centrobolus fulgidus* and *Gnomeskelus tuberosus microdens*) occurred in both edge and core assemblages throughout all the regenerating and unmined sites. Only a few species were identified as discriminating and occurred only in the edge assemblage in the rehabilitating sites (e.g., *Orthoporoides* sp.). *Orthoporoides* sp. occurred in both the edge and core assemblages in the unmined forest, probably due to some habitat or diet preferences not provided in the core areas of the rehabilitating forests. The MDS results of the 10-year-old regenerating site, grouped 0 meters with 40, 60, and 80 meters. In this site the occurrence of *Doratogonus* sp., *Juliaformia* sp. 3, and *Orthoporoides* sp. is responsible for the dissimilarity between the edge and core assemblages. The difference in contribution of the same species to the edge or core assemblage between the study sites may be ascribed to several factors that have not been investigated as part of this study. For millipedes the differences in the width of edges between sampled sites may be due to increasing variation in the physiognomic structure with an increase in regeneration age, implying increases in structural heterogeneity and soil organic content (see van Aarde et al. 1998). This is not surprising, however, because the rehabilitating area is considered to be following a pathway of secondary succession (van Aarde et al. 1996a). During secondary succession the structural heterogeneity of a site will increase due to the formation of subcanopy layers and increasing gap formation (Bierregaard et al. 1992). These gaps cause a mosaic of different successional stages occurring within one aged site, and succession within these gaps causes changes in biotic and abiotic variables.

In the younger rehabilitating sites where the vegetation is more homogeneous and less dense, the sites lack variation intrinsic to the older rehabilitating sites.

Edges are considered an important factor affecting the recovery of species richness, species composition, and species diversity of disturbed areas (Finegan 1996). Although numerous studies have been conducted on biotic and abiotic edge effects (Bierregaard et al. 1992), no definite edge effect pattern has been identified. A major criticism of edge effect studies is that they are too simplistic, expecting a uniform pattern of effects on all ecological levels (Murcia 1995). However, it is likely that edge effects interact with each other and will therefore be neither linear nor monotonic (Murcia 1995). The generality of the edge concept should be approached with caution when dealing with taxa comprising species with such diverse natural histories as in the present study. Furthermore, one should also be cautious when describing the benefits of edges to wildlife, particularly when dealing with species that require forest interior for survival (Yahner 1988).

Although no specific trend in the estimated community variables with increasing regeneration age could be identified, differences between sampling sites were apparent. In some cases roads cause the assemblages to have unique species; in other circumstances it is merely a change in abundance of the constituent species. Edges also may explain some of the differences in community characteristics between rehabilitating and unmined coastal dune forests.

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