Distribution and abundance of rodents, millipedes and trees in coastal dune forests in northern KwaZulu-Natal

By

Leon-Jacques Theron

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Leon-Jacques Theron

Supervisor: Prof. R. J. Van Aarde
Conservation Ecology Research Unit
Department of Zoology and Entomology
University of Pretoria
Pretoria, 0002
South Africa

ABSTRACT

A widely observed pattern in nature is a positive relationship between local abundance and spatial distribution. This study investigates this relationship amongst three taxa namely rodents, millipedes and trees on regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal. No sensible analyses were possible on the rodent data. Both millipedes and trees had a positive relationship between local abundance and distribution (measured as species incidence). Millipedes showed no changes in the relationship with changes in habitat regeneration time. For trees, the regression slope decreased with time due to changes in abundance and incidence of *Acacia karroo*. Lack of bimodality in incidence frequency distributions ruled the core-satellite metapopulation hypothesis out as a mechanism producing the positive abundance-incidence relationship. The resource availability hypothesis was a most likely mechanism. This study confirmed that rare species tend to be restricted in both abundance and incidence.

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CHAPTER 1

INTRODUCTION

LITERATURE REVIEW

Rank-abundance models

One of the simplest ways to characterise a community or assemblage is by counting the number of species present in a given area (Begon *et al.* 1990). However, valuable information will be lost this way and it is doubtful whether such a method makes ecological sense (Begon *et al.* 1990, Zobel & Liira 1997). Therefore, the structure and organisation of communities are often described using species rank-abundance graphs (Begon *et al.* 1990, Tokeshi 1993). By using this method it is possible to determine which species are dominant with regards to abundance and also to deduce the pattern of resource division within a community (Tokeshi 1993).

Models that have been proposed to explain community structure based on species abundance patterns include the log-series, log-normal, hierarchical niche breakage, broken-stick and Zipf-Mandelbrot models (Tokeshi 1993). These models are either statistically or biologically orientated. The log-normal model has been shown by May (1975 in Tokeshi 1993) to be a statistical consequence of large numbers resulting from the central limit theorem. That is, the distribution of means from a non-normal population will tend towards normality as the number of samples (n) increases (Zar 1996). With no biological mechanisms playing a role in the resulting pattern, it seems to have no biological meaning.

In searching for a biological explanation of species abundance patterns several niche-based models have been developed (Figure 1). These models presume either an equilibrium or a stochastic state of a community. The broken-stick model is an example of an equilibrium based niche model (Tokeshi 1993). Here the total niche is compared to a stick broken at (n – 1) randomly scattered points along its length. A group of (n) species, with equal competitive ability, simultaneously occupies the total niche and these compete with each other for a portion of the total niche space. The species securing the largest portion will have the highest abundance. Claims have been made that the model fits certain animal populations, but the broken-stick model is not falsifiable (Wilson 1993).

As it is based on a random process all possible rank-abundance lists are equiprobable and therefore no single community can support or cast doubt on it (Wilson 1993). The only way to test it is with replicate communities that do not exist in nature, as no two communities will have the same number of species (Wilson 1993). Another niche-based example is Tokeshi's (1990) dominance pre-emption model (Figure 1 & 2). Here the first competitively superior species occupies more than half of the total niche. The second species takes more than half of the remaining portion and so on. This results in a single dominant species securing more than half of the available resources for itself. Fitting these models to real data remains problematic, as observed patterns may be due to statistical artefacts or sampling methodology (Wilson 1993). The dominance of a species may not always be projected as the highest abundance, but in the case of sessile species could also be expressed as biomass or ground cover (Begon *et al.* 1990). In general these models are spatially and temporally ill defined. Basing species abundance models on the niche concept makes them difficult to falsify and to determine underlying biological mechanisms. Rank-abundance models have therefore given little insight to our understanding of natural patterns (Wilson 1993).

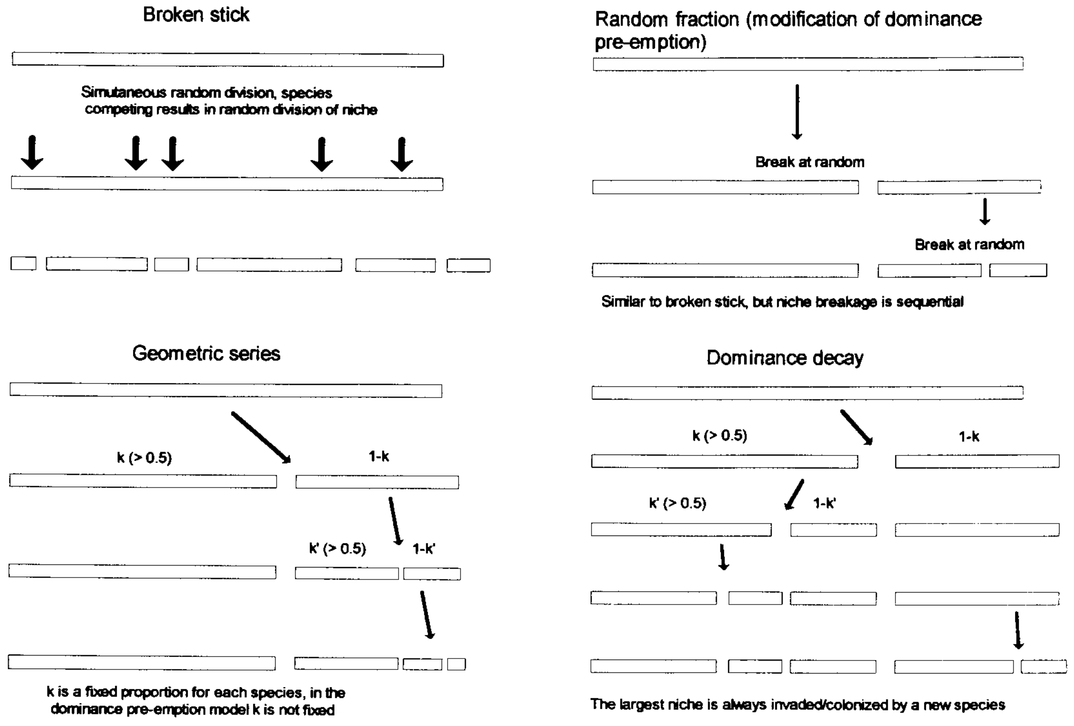

Figure 1. Schematic representation of rank-abundance models (modified from Tokeshi 1993).

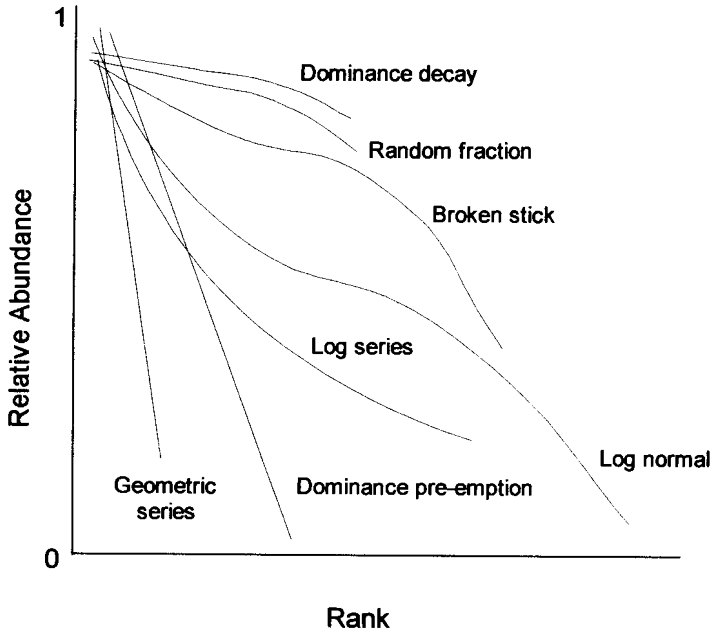

Figure 2. Rank-abundance patterns of various models (modified from Tokeshi 1993)

Abundance-distribution relationships: An overview of mechanisms

The study of species abundance and distribution is considered the central theme of ecology (Hanski *et al.* 1993, Naeem 1996, Krebs 1999). Several empirical studies have noted a positive relationship between the spatial distribution and abundance of species (Gaston 1996a). Species that occur at high abundances on any given patch are to be found on more patches in a region than species with a low abundance (Nee *et al.* 1991). This phenomenon has been reported for a variety of taxa, habitats, geographic regions and spatial scales (reviewed by Brown 1984, Gaston 1996a). Abundance-distribution studies differ from rank-abundance studies by incorporating aspects of species distribution, be it over the entire range of a set of species or at local spatial scales. Using this approach factors such as rarity and dominance now acquire a spatial aspect.

However, it has been suggested that the observed pattern is not real, but simply a sampling artefact (see Gaston *et al.* 1997a). If sampling is insufficient then species occurring at low densities will tend to be overlooked, producing a positive abundance-distribution relationship. Similarly, phylogenetic non-independence could also result in a positive interspecific relationship (Harvey & Pagel 1991). If species are phylogenetically very closely related, that is they share a very recent common ancestor, they may fail to represent independent data points. This will inflate the degrees of freedom for testing statistical significance, therefore producing a false positive relationship. Many authors have argued that the relationship is not a sampling artefact (e.g. Hanski 1982, Brown 1984, Nee *et al.* 1991, Gaston 1996a, Venier & Fahrig 1996 and Collins & Glenn 1997). Indeed Hanski (1982) goes as far as saying that a correlation between abundance and distribution is the rule in nature, although there are truly rare species with a wide distribution. Several intensive studies, both on local and continental scale, and covering several taxa, refute phylogenetic interdependence. These studies include a census of American birds (Bock & Ricklefs 1983, Brown 1984), British birds together with several other taxa (Gaston 1996a), four different taxa at Konza Prairie (Collins & Glenn 1997), Iberian Caraboidea (Gutierrez & Menendez 1997) and Australian frogs (Murray *et al.* 1998). It has even been observed for microcosm experiments (Gaston & Warren 1997, Warren & Gaston 1997, Gonzales *et al.* 1998). Given this evidence there must be some biological explanation for the relationship. A discussion of some of the biological mechanism proposed to explain abundance-distribution patterns follows below.

Metapopulation dynamics

A metapopulation is an assemblage of local populations connected by migration (Levins 1970 in Hanski & Gyllenberg 1993). The geographic range of a metapopulation is therefore made up of local populations occupying suitable patches throughout the range. Survival of the species is dependent on the rate at which full patches colonise empty patches and the rate at which populations go extinct on occupied patches. Thus, the higher the colonisation rate and the lower the extinction rate, the more patches the species will occupy. Levins' model of metapopulation dynamics (1969 in Collins & Glenn 1991) is described by the equation:

$$\frac{dp}{dt} = cp(1-p) - ep,$$

where p is the fraction of patches occupied by a species, c is the rate at which individuals of full patches occupy empty patches and e is the rate at which a population of a species goes extinct on a patch. The model produces a unimodal frequency distribution of species site occupation with the mode at $0 \leq p \leq 1$ (Collins & Glenn 1991, Figure 3). The model does not, however, predict a positive relationship between abundance and incidence (Gotelli & Simberloff 1987).

At equilibrium the number of patches occupied will be given by $p = 1 - \frac{e}{c}$

The distribution and abundance of species is therefore a result of dispersal dynamics and successful occupation of empty patches. This in turn depends on intrinsic characters of a species such as reproductive rate, resource utilisation, dispersion and competitive ability. Apart from competition these facets can be readily investigated and defined by the ecologist. Because the distribution of species is included, the model is spatially explicit and the structure of a community or taxonomic assemblage can be empirically investigated along well defined population characteristics such as reproductive rates and dispersion (Nee *et al.* 1991).

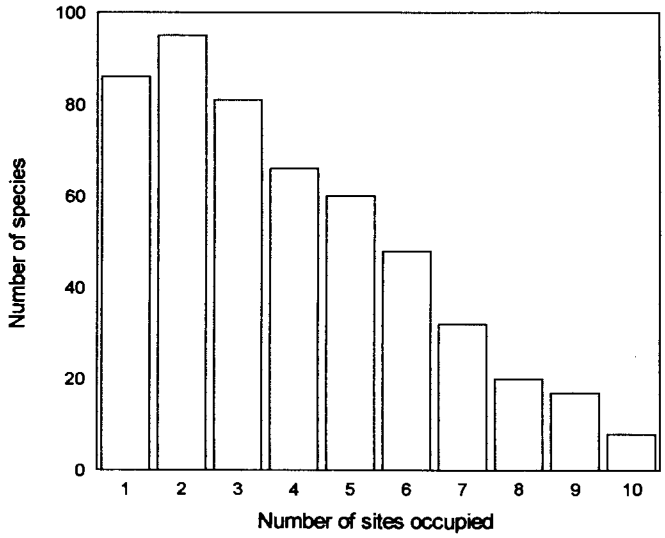

Figure 3. Bar graph of species site occupation frequency distribution for Levins' (1970) metapopulation model adapted from Gotelli & Simberloff (1987).

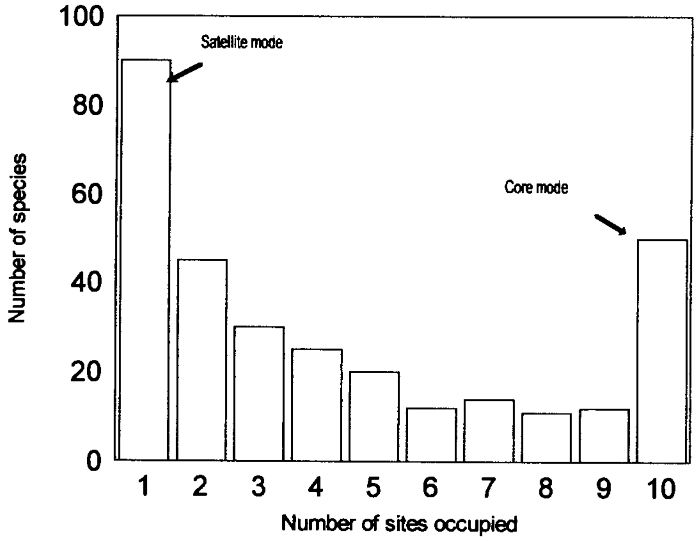

Figure 4. Bar graph of species site occupation frequency distribution for Hanski's (1982) core-satellite hypothesis. Note the satellite and core modes.

Hanski (1982) developed a stochastic version of Levins' model for which extinction and colonisation are dependent on the number of patches occupied. Therefore, the extinction rate on each patch will decrease as the number of occupied patches increases. It predicts a bimodal regional distribution of species with modes at the lowest and highest number of sites (Figure 4). The model produces a mode of so-called satellite species, (occurring at less than or equal to 10% of sites) and a second mode of core species (occurring at more than 90% of sites). The model also presumes that sites are equally favourable for all species (Brown 1984). Species randomly fluctuate between the core and satellite mode, with species occurring at the centre showing the highest variance. Support for his model has come from work on mangrove island insects (nine sites), plants around old houses in Russia (12 sites) and species of *Onthopagus* in tropical, lowland forests (10 sites) (Hanski 1982). However, Gaston & Lawton (1989) found no evidence for core-satellite switching in a bracken herbivore community.

Brown (1984) criticised the model on the grounds that it is highly unlikely that sites or patches are equally favourable for all species. Considering the model only holds for species that are ecologically closely related (Hanski 1982), the overriding factor producing differences in distribution and abundance will be variation in habitat (Brown 1984). Brown also argues that the bimodal distribution found in the data sets analysed by Hanski is an artefact of sampling a small number of sites.

Collins and Glenn (1997) also found a bimodal core-satellite distribution for several, though not all, taxa sampled over a relatively small area of 36 km^2. However, increasing the spatial scale, resulted in a unimodal distribution for all taxa. Gotelli and Simberloff (1987) and Van Rensburg *et al.* (in press) also found bimodality disappeared when sample size or area was increased. Nee *et al.* (1991) argued that the extinction rate on individual patches will only decrease as patch occupation increases if patches reach their maximum population size instantaneously. Extinction also happens instantaneously. Rather, patches with larger population sizes will have smaller extinction probabilities and/or higher dispersal rates. Therefore at equilibrium they will occupy more patches than a species with smaller population sizes (Nee *et al.* 1991).

As satellite species occupy so few patches, and the model suggests they will have very high extinction probabilities, they require continuous colonisation from patches outside the region to survive. Hanski (1982) called this the rescue effect. If satellite species are truly rare the chances of such continuous colonisation taking place is small (Brown 1984). The core-satellite hypothesis therefore is a result of under sampling and incorrect metapopulation assumptions (Brown 1984, Nee *et al.* 1991).

Nee *et al.* (1991) proposed the carrying capacity hypothesis, in which all patches are considered equal, hence all species have the capacity to occupy all patches. Species differ in the carrying capacities they can attain on patches. Higher carrying capacities will result in higher colonisation rates and lower extinction rates. Hence locally abundant species will have a wider distribution, that is a positive relationship between abundance and distribution. In accordance with other metapopulation models it embodies a dynamic link between local abundance and regional distribution (Gaston *et al.* 1997a). Differences in resource availability or resource utilisation could generate interspecific variation in carrying capacities (Nee et al. 1991).

All metapopulation models assume that all the species in a taxonomic assemblage exhibit metapopulation dynamics. If this is not true, then the positive abundance-distribution relationship should breakdown (Gaston *et al.* 1997a). Empirical evidence currently suggests that most plant and vertebrate species do not exhibit metapopulation dynamics, yet the positive abundance-distribution relationship persists (Gaston *et al.* 1997a).

Range position and niche/resource breadth

Brown (1984) argued that the abundance-distribution correlation is due to variation in the abundance of species throughout their specific range and not to metapopulation dynamics. Brown noted that several empirical studies have shown a normal or near normal distribution of species along an ecological gradient, resulting from spatial auto correlation. Consequently species will be more abundant in the centre of their range, decreasing towards the edges (Hengeveld & Haeck 1982, Brown 1984, Brown *et al.* 1995). Measuring abundance and distribution in any given area, some species will be in the centre of their range, while most will be at the edge. This results in some species having a high abundance and wide distribution, whilst others will be locally rare (Brown 1984). However, looking at abundance patterns at the continental scale, at which the entire ranges of species are often incorporated, a similar pattern will emerge, albeit for different reasons.

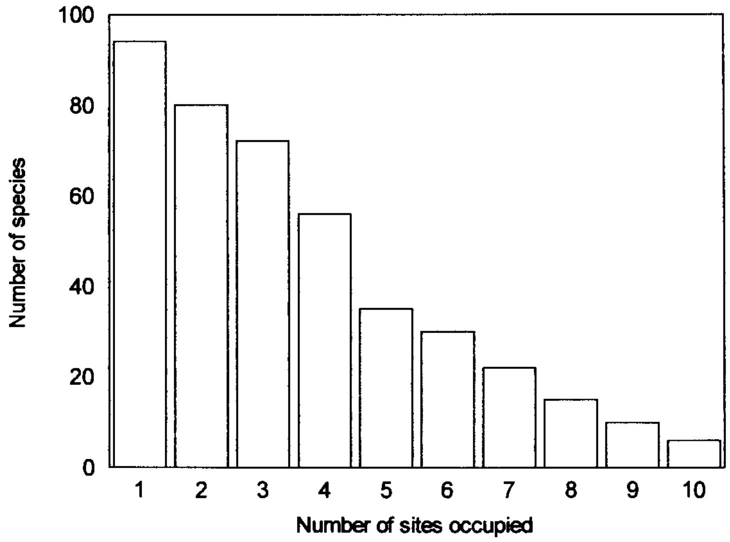

Figure 5. Bar graph of species site occupation frequency distribution for Brown's (1984) niche breadth hypothesis (adapted from Collins & Glenn 1991).

Brown (1984) argued that for situations that incorporate entire ranges of assemblages, certain species will have a wider distribution and higher abundance because they have broader niches; that is they utilise a wider variety of resources/habitats. The hypothesis produces a unimodal site occupation frequency distribution (Figure 5). Species occupying the mode will have narrow niches. If niches are multidimensional and environmental variation is autocorrelated, a positive abundance-range size relationship should be observed (Gaston *et al.* 1997a). Species that have broad niches and high environmental tolerances will achieve high local abundances and will be widespread and ecological specialists will never be very successful. It is, however, easy to imagine a species that is specialised in utilising a few, widely distributed resources (Gaston *et al.* 1997a). Although specialised it should also attain high local abundance and a wide distribution.

Seagle and McCracken (1986) found no correlation between niche breadth and abundance for four terrestrial taxa. If abundance is measured across several habitat types, and niche breadth measures habitat selection, there should be a positive correlation between niche breadth, abundance and distribution (Hanski *et al.* 1993). For the niche breadth hypothesis to hold niche breadth should determine both distribution and abundance. This exposes one of Brown's assumptions - there should be little spatial variation in the niche of a species. Species, however often show local adaptation (Gaston *et al.* 1997a). If a species utilises a wide range of resources regionally, but in a certain locality it has adapted to utilise a narrow band of resources, there is no reason why it should attain a higher abundance in the specified locality compared to a species that utilises an equally narrow set of resources both at the locality and regionally (Gaston *et al.* 1997a). A further reason for this might be incorrect measurement of niche axes (Gaston *et al.* 1997, Gregory & Gaston 2000). It is difficult to measure the multidimensional niche of a species, let alone that of several species in a taxonomic assemblage. Thus, it can not be falsified and has very little empirical evidence (Gaston *et al.* 1997a). The argument is circular and defining niches for a range of species is problematic.

Resource and habitat availability

Venier & Fahrig (1996) have proposed habitat availability as the cause for a positive relationship between distribution and abundance. A theoretical landscape consisting of breeding and non-breeding cells where individuals may randomly die, move from one cell to another or reproduce within each time step is used as a model. It begins with 500 individuals and cells are saturated at 10 individuals per cell. Probability of extinction is higher on non-breeding cells than on breeding cells. The critical parameter is the proportion of landscape occupied by breeding habitat. Populations in landscapes with less than 5% breeding habitat went extinct within 500 simulations. All other populations stabilised over time. Breeding habitat was positively correlated with abundance and distribution. Populations utilising landscapes with a high proportion of breeding habitats had high abundance and distribution values. Generalist species, that utilise more common habitats or more habitat types within a landscape, will have a wider distribution and be more abundant.

The resource breadth hypothesis follows a similar rationale, based on locally abundant and widely dispersed species which utilise resources that are widely distributed and abundant (Hanski *et al.* 1993, Gaston 1994). Blackburn *et al.* (1996) investigated the relationship between life history and abundance of British birds. They found that species with high abundances had a faster rate of growth, either absolute or relative to their body size. They argue that in order to achieve fast growth rates adults will have to provide food at a fast and reliable rate. This in turn depends on a reliable, abundant food resource. In this case species that specialise on widespread resources can also attain a high local abundance and wide distribution. Gregory and Gaston (2000) subsequently established that bird species with a high local abundance and wide distribution do in fact utilise widely distributed resources and habitats.

The above two theories are very similar and share some points in common with Brown's (1984) niche breadth hypothesis, but the focus is shifted from an organismal to a habitat or resource perspective. In the case of the habitat selection hypothesis, either the availability of suitable habitat, or the use of different habitat types can result in positive distribution-abundance relationships. Unlike the niche breadth hypothesis both specialists and generalists can attain wide distributions. The same is true for the resource availability hypothesis. Both these hypotheses are a more parsimonious explanation of the relationship, as no assumptions need to be made about niche breadth (Gaston *et al.* 1997a).

Vital rates

Holt *et al.* (1997) proposed a non-spatial model for generating a correlation between distribution and abundance. The model predicts that if a set of species are similar in their responses to density-dependent processes, but differ with regards to spatially and density-independent factors, they should automatically exhibit a positive relationship between distribution and abundance. The model is only concerned with a subset of species characteristics in which birth and death rates drive local population dynamics as opposed to dispersal, which is the overriding parameter in the metapopulation models. The model does not necessarily have to compete with the metapopulation models but may explain the pattern in taxa where metapopulation dynamics are absent (Holt *et al.* 1997). It only holds for areas where all the species have had sufficient time to disperse to those sites where they can potentially persist, and therefore exist in some kind of equilibrium state. As the effects of dispersal can be neglected, the distribution or range of a species is taken as the set of sites where birth rates exceed death rates (Holt *et al.* 1997).

Formally, the model predicts that if species differ (1) solely in rates of density-independent mortality; (2) have similar spatial variation in birth rates and; (3) different habitats are equally available (a smooth environmental gradient is given as an example), then range size will be directly proportional to local abundance. Graphically the model looks as follows (Figure 6):

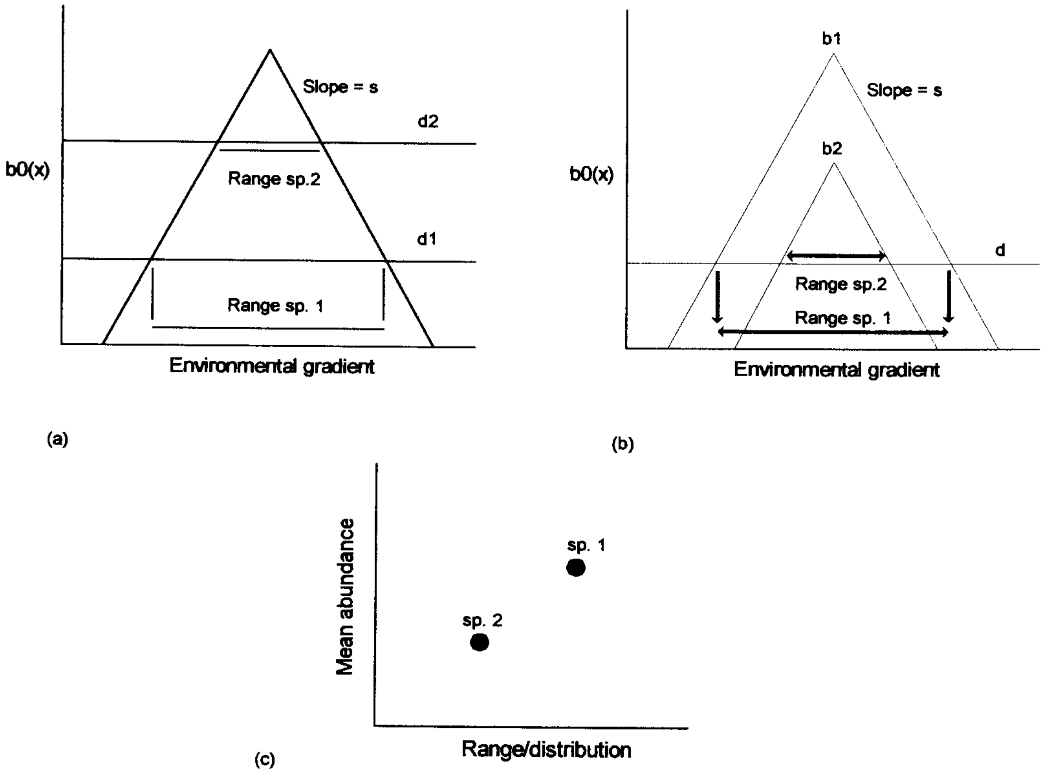

Figure 6. a) Birth rates (b_0) at each site (x) along an environmental gradient decline linearly away from the optimum site (slope s). Species 1 and 2 have different density-independent death rates (d_1 and d_2). **b)** Decline in birth rate (s) is constant, but species 1 and 2 have a spatially uniform difference in maximum birth rate (b_1 and b_2). **c)** Both a) and b) give rise to the same positive relationship between mean abundance and range size (Holt *et al.* 1997).

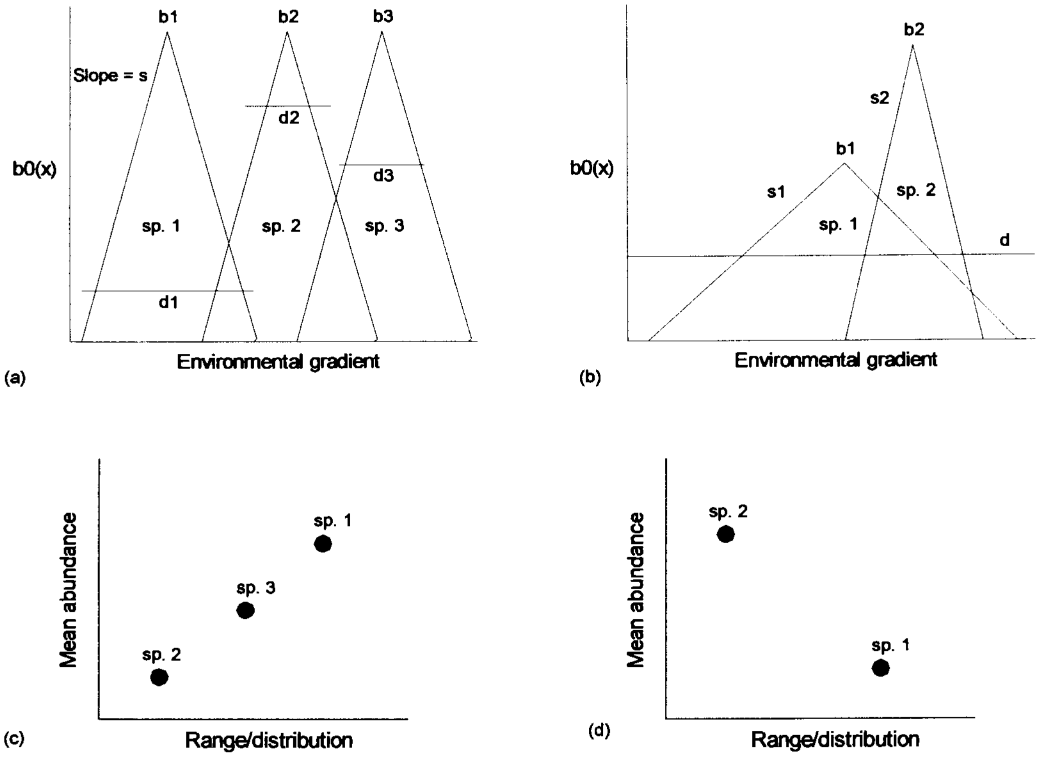

Figure 7. a) Three species experience maximal birth rate (b_1, b_2 and b_3) at different points along a gradient but show the same spatial decline in birth rate (s is constant), and each have a different density-independent death rate (d_1, d_2 and d_3); resulting in **c)** - a positive relationship between mean abundance and range size. **b)** Species 1 and 2 show great variation in decline of birth rate (s_1 and s_2) as well as maximum birth rate (b_1 and b_2), but a similar death rate (d); resulting in **d)** - a negative correlation between mean abundance and range size (Holt *et al.* 1997).

The vital rates hypothesis has one distinct advantage over all the hypotheses discussed so far - it can explain a negative relationship (Figures 7b & d). Though not commonly found, this pattern has been observed. Gaston and Lawton (1990) suggested that a negative relationship would result when the sampled habitat differs markedly from the surrounding available habitats. They compared bird abundance and distributions in a common European habitat (oak woods) and a rare habitat (Handa Island), comprised mostly of cliffs. Abundance was positively correlated with distribution in the oak wood site and negatively for the Handa site. It is possible that widespread species may only attain low local abundance in the rare site, producing such a negative relationship (Gaston & Lawton 1990).

Conversely, it is also likely that species adapted to the rare habitat will not attain high abundances in other habitats. Another possibility is that the species assemblage (birds) at Handa show marked interspecific ecological variation i.e. raptors might be widespread, but rare, whereas passerines might show the opposite pattern. Dividing the assemblage into trophic guilds might produce a positive correlation within each guild.

Species rank-abundance models have yielded little insight in ecology in general (Wilson 1993). The models are difficult to fit and it is not known how species in a given area divide the available resources (Wilson 1993). Whether communities exist along the lines described by rank-abundance models is questionable (Wilson 1991). However, if data fit a specific rank-abundance model it does not explicitly imply that resource division took place as stipulated by the model, as the pattern could also result from a statistical artefact.

Unlike rank-abundance models, which invoke how resources are divided based on niche hyper-volumes, the abundance-distribution relationship has stimulated much thought and investigation into continental, regional and local scales of species patterns. With these contemporary models, we are now much closer to answering one of Darwin's questions of why certain species are widely distributed and common, and others are rare and narrowly distributed (Gaston *et al.* 1997a).

Several of the proposed biological models have merit. The models of Brown (1984) and Hanski (1982), however, have very little empirical support. The model of Hanski (1982) also suffers from incorrect assumptions. Interestingly Brown's hypothesis is based on niche breadths. The other models discussed need not be mutually exclusive, but rather compliment each other. Although vital rates are governed by the physiology of a species, habitat and resource availability do play a role in determining the slope of birth and death rates. Where metapopulation dynamics apply, habitat availability will determine if successful colonisation takes place. In turn birth and death rates will also contribute to dispersal rates.

RATIONALE FOR THE PRESENT STUDY

The mining and subsequent rehabilitation of coastal dunes at Richards Bay provides an opportunity to study the interspecific abundance-distribution relationship and site occupation patterns across a wide temporal range. As distribution often refers to the entire ranges of species, from here onwards I will use the term incidence to describe the spatial distribution of species, as the scale of this study did not incorporate the entire ranges of species. The abundance-incidence relationship represents the dynamics of an assemblage; abundance is the net result of population growth processes and incidence represents the constraints of the physical environment on species (Boeken & Shachak 1998). Underlying incidence frequency distribution patterns form an important part in explaining abundance-incidence relationships (Hanski 1982, Hanski & Gyllenberg 1993, Brown 1984 and Collins & Glenn 1997) and can be of assistance in identifying possible mechanisms.

Several studies have found age related unidirectional changes in species diversity, richness and community structure on rehabilitating coastal dune forests at Richards Bay (Mentis & Ellery 1994, Van Aarde *et al.* 1996a, Van Aarde 1997, Kritzinger & van Aarde 1998). Investigating the relationship between incidence and abundance in rehabilitating stands of different ages may shed light on whether this pattern does in fact exist in newly developing assemblages as well as whether it changes with regeneration age. Maurer (1990) predicted that the abundance-incidence relationship should increase in slope as habitat productivity increases. At present there is no information on the productivity of coastal dune forests at Richards Bay, but a change in the slope of abundance-incidence relationships between stands of different ages, for several taxa, may hint at changes in habitat productivity. An investigation of incidence-frequency distributions may help determine which mechanisms are contributing to observed abundance-incidence patterns. These incidence-frequency distributions may also contribute to our knowledge of the dispersal ability of higher taxa (Collins & Glenn 1997). Any within-taxon changes in frequency distributions between different aged stands could be a result of temporal scaling. That is, as organisms have more time to disperse, the percentage of rare species will decrease.

Further, the most difficult task ahead for ecologists is to determine the relative contributions of each of the proposed mechanism to one of the most general and robust patterns in nature (Gaston *et al.* 1997a). This requires sound data on not only abundance and incidence, but also dispersal, habitat utilisation and vital rates of species.

AIMS

This study aims to investigate the relationship between species abundance and incidence for rodents, millipedes and trees within four different seral stages of coastal dune forest development. It includes regenerating stands of known ages, ranging from 13 years to a forest patch more than 60 years old.

NULL HYPOTHESES

The following null hypotheses have been formulated:

1. No structural relationship exists between species abundance and incidence.

2. Stand age has no effect on species abundance and species incidence.

3. Stand age has no effect on incidence-frequency distributions.

4. There are no between-taxon differences in incidence frequency distributions.

KEY QUESTIONS AND PREDICTIONS

- Does any structural relationship exist between the incidence and abundance of species?
- If the case that it does, is this structural relationship positive or negative?

I predict a positive relationship between incidence and abundance for each taxon. That is species that occupy a high number of sample sites will have a higher average abundance than species that occupy fewer sites (Hanski 1982, Brown 1984, Gaston 1996a).

- Does it develop over time?

I predict that the slope describing the abundance-incidence relationship should increase with a decrease in stand age based on the assumption that young regenerating stands should have pioneer species with higher average abundance and incidence compared to species in older stands.

- Does the abundance of species with similar incidence change over time?
- Does the incidence of species with similar abundances change over time?

I predict that species with low incidence would have a higher abundance in the older stands, based on the assumption that with an increase in regeneration age, species should have more time to increase in numbers. On the other hand it would be expected that high incidence species in the regenerating stands consist of pioneer species that should decrease in abundance with increasing regeneration age. It is expected that incidence would increase with stand age for corresponding abundance classes, based on the assumption that species in the older stands would have had more time to disperse.

- Do incidence frequency distributions of taxa change over time?

Here I predict that taxa in the younger stands should show bimodal occupancy distributions based on the rationale that taxa in the younger stands would consist of two main groups of species, firstly recently established species with restricted incidence and secondly, pioneer species with a high incidence. I predict that younger stands should have a higher number of satellite species than older stands based on the assumption that a large percentage of species in the younger stands have not yet had sufficient time to disperse.

- Are there between taxon differences in incidence frequency distributions indicating possible differences in dispersal ability?

Based on the organismal scaling rationale of Collins & Glenn (1997) I predict that better dispersing taxa would have more core species than poorer dispersing taxa.

CHAPTER 2

STUDY SITE

LOCATION AND CHARACTERISTICS

The study was conducted on coastal dunes regenerating in response to a post-mining rehabilitation programme, situated north of Richards Bay (28°43'S, 32°12'E) and an unmined forest south of the Cape St. Lucia Lighthouse (28° 30' S 32° 24' E). Since 1977 the area has been strip mined for zircon, ilmenite and rutile by Richards Bay Minerals. The study site falls within the Maputaland Centre of the Centres for Plant Diversity (WWF & IUCN 1994). This centre stretches from the Limpopo River in southern Mocambique to Lake St. Lucia in the south, where it extends along the coast to Mtunzini. This centre for plant diversity is also bound to the west by the Lebombo Mountains and the east by the Indian Ocean. Almost 10% of the region is conserved, although 93% of the conserved area is concentrated in the savannah vegetation in the northern parts (WWF & IUCN 1994). Agriculture, expanding urban development, dune mining, aforestation and invasive alien plants are considered major threats to the area (WWF & IUCN 1994).

The first sea-facing dune was not included in the study as Venter (1972, 1976) showed that it consists of a different plant community to the second dune. The first dune is also not mined and may serve as a source area for the colonisation of mined dunes (Van Aarde 1997). Apart from the mining, dunes are subjected to a variety of other disturbances ranging from cattle grazing to collection of medicinal plants and wood (personal observation).

The study site consists of a successional sere comprising a number of seral stages of known age. Data for the study were collected from three regenerating stands that were 12-14, 15-17 and 18-20 years old at the time of sampling (July 1998 - March 1999). The median ages of the regenerating stands will be referred to throughout the present study. Surveys were also conducted on an unmined stand just south of the Cape St. Lucia lighthouse (Figure 8). This stand is considered representative of relatively undisturbed coastal dune forest. Inspection of aerial photographs dating back to 1937 indicated no major disturbances in the area up to the time of this study, suggesting it is older than 60 years.

The regenerating stands are situated 12 and 20 km north-west of Richards Bay (Figure 8). The unmined stand is situated approximately 21 km north-west of the 19 year old stand (i.e. 41km north of Richards Bay). The stands vary in size as follows: 35 ha (13 years old), 46 ha (16 years old), 20 ha (19 years old) and 34 ha (unmined stand).

CLIMATE

The climate of the study area is hot and humid, with no frost occurring. The average maximum temperature at Richards Bay (28° 48' S 32° 6' E) is 26.2 °C, with an average minimum of 17.3 °C (South African Weather Bureau[1]). The hottest month is January with an average maximum temperature of 29.2 °C. The average maximum relative humidity at 08:00 is 82 % dropping to an average of 67 % at 14:00. April has the highest maximum relative humidity (87 %). Average annual rainfall for Richards Bay is 1228 mm. January has the highest average monthly rainfall of 172 mm and June the lowest, namely 57 mm (South African Weather Bureau[1]).

Average maximum and minimum temperatures at Cape St. Lucia Lighthouse (28° 30' S 32° 24' E) are 24.7 °C and 17.8 °C respectively (South African Weather Bureau[1]). January has the highest average maximum temperature of 28.0 °C. Average annual rainfall at Cape St. Lucia is 1424 mm. January has the highest average monthly rainfall of 164 mm.

MINING AND REHABILITATION

After strip mining, dunes are reshaped, the topsoil replaced and vegetated with various annual species. Shade cloth windbreaks are erected to prevent wind erosion of bare dunes. After this process has been completed the shade cloth is removed and the dunes are left to regenerate of their own accord (Van Aarde *et al.* 1996a). The purpose of the operation is dune rehabilitation and not restoration (Van Aarde 1997).

Mentis and Ellery (1994) showed that the succession taking place on regenerating dunes was similar to that found in surrounding disturbed areas not exposed to mining. Vegetation regeneration on these dunes was associated with unidirectional changes in species richness and diversity of several different taxa and the process has not yet stagnated or reversed (Van Aarde *et al.* 1996a). The woody vegetation of the oldest regenerating stand is dominated by *Acacia karroo*, but forest trees are returning to the lower strata (Van Dyk 1997).

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[1] South African Weather Bureau, Department of Environmental Affairs and Tourism, Pretoria 0001

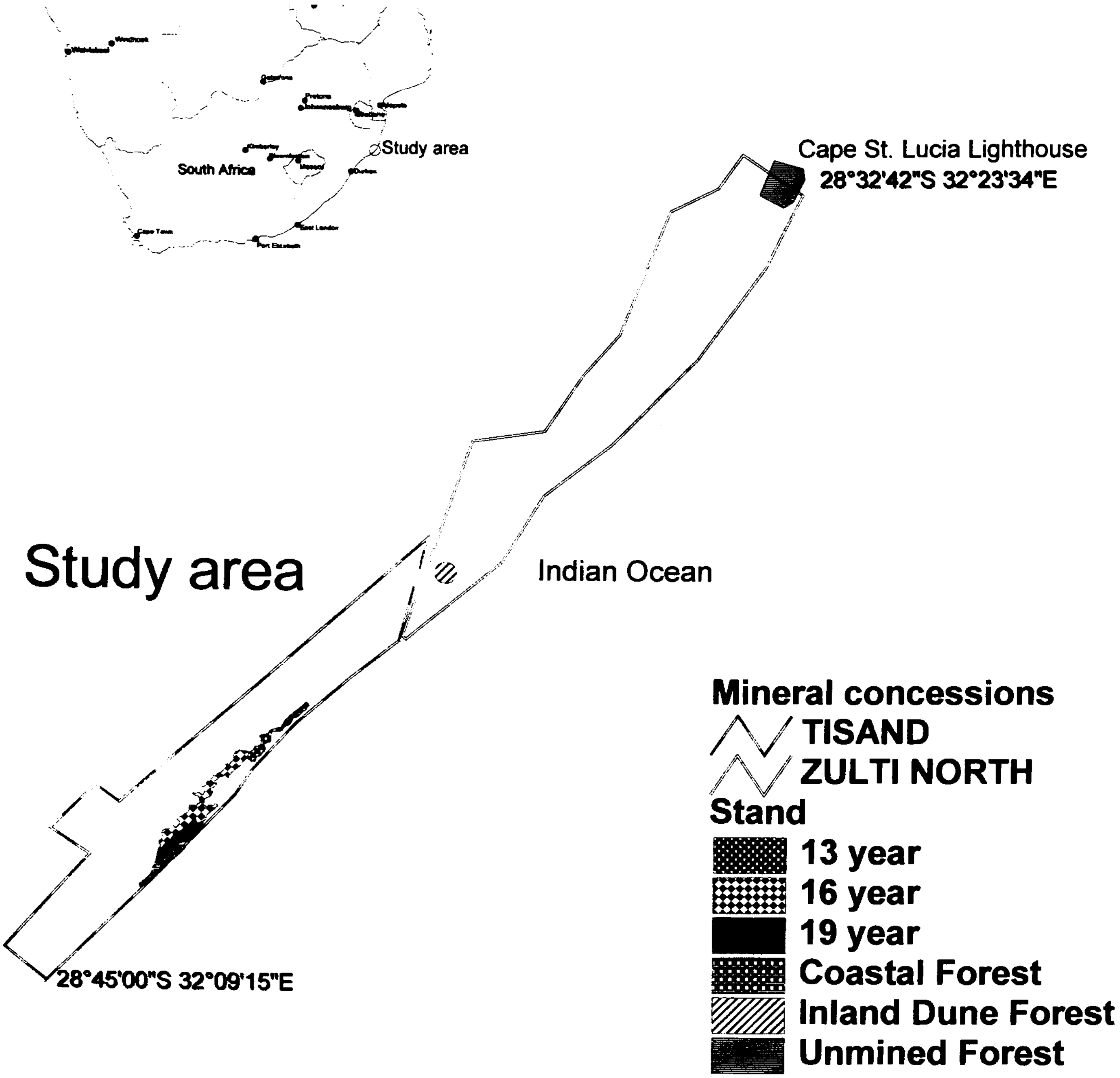

Figure 8. Map of the study area north of Richards Bay (28°43'S, 32°12'E), KwaZulu-Natal, illustrating mining lease area, regenerating and unmined stands of coastal dune forest. Map not according to scale.

CHAPTER 3

MATERIALS AND METHODS

DATA COLLECTION

Rodents

Rodents are trapped annually in the study area as part of a long term monitoring program. The sampling is conducted during February and August and involves trapping on three permanent grids in each of the different aged stands. A grid consists of 49 trapping stations (7 × 7), each located 15m apart. A Sherman live trap (7.5 × 9.0 × 23.0cm) is placed at each station.

In order to avoid duplication, sampling for this study was coincided with the February monitoring session. To increase the number of sites sampled three more grids were placed out in the four stands, for which grid layout and trapping regime were the same as the long term monitoring program. Grids were placed at least 200m apart, far enough to ensure independent sampling. Traps were baited with a mixture of peanut butter and raisins and left out for three consecutive nights. Each trap was inspected and rebaited every morning at dawn. All animals caught were identified to species level and individually marked by toe clipping.

Millipedes

Millipedes are also sampled annually as part of an on going monitoring program, which takes place during December and January. The sampling does not, however, take place on permanent quadrats, but rather on randomly placed quadrats within each stand. Millipedes are counted in quadrats measuring 35 × 6m, as Van Aarde *et al.* (1996b) found these rectangular quadrats were easier to sample than square quadrats of equivalent size. Six quadrats are sampled in each rehabilitating stand as well as in the unmined area.

To avoid unnecessary replication the present survey was incorporated into the monitoring program. The number of quadrats was, however, doubled to 12 in each stand. An additional six quadrats in each stand were sampled in January 2000. The size of the quadrat necessitated the use of more than one surveyor and three or more surveyors were used at all times. Quadrats were measured out using a tape measure and the corners and midpoints marked with marker poles.

All millipedes in the quadrat were counted, except for arboreal specimens occurring above a height of 3m, as these could not be identified with any certainty. Millipedes were initially placed in morpho-species classes as determined by Van Aarde *et al.* (1996b). Voucher specimens of each class were collected and preliminarily identified by Michelle Hamer[2] of the Natal Museum, Pietermaritzburg. The majority of millipedes found in the area are relatively large (60 - 160mm) and conspicuously coloured, which facilitated their counting. To minimise surveyor fatigue, sampling time per quadrat never exceeded 45 minutes. However, in some cases where sampling took place in very dense vegetation, this measure was violated.

Trees

In a previous study on tree communities on the regenerating stands at Richards Bay conducted by Van Dyk (1997), the point centre quarter method (Cottam & Curtis 1956) was used. This is a plotless sampling method and is therefore not suitable for this specific study as it does not explicitly measure site occupation. A quadrat based method was thus used for surveying tree species. To determine quadrat size, a pilot study was undertaken in the 19 year stand. All trees above my shoulder height (1.7m) were counted and identified to species level in 15 randomly selected quadrats. Each quadrat was increased stepwise in size from 2m × 2m to 16m × 16m. Species accumulation curves were plotted, for which the number of species recorded levelled off before the largest quadrat size (16m × 16m). Therefore 16m × 16m plots were used for the duration of the tree survey, following the nomenclature of Arnold & De Wet (1993). Quadrates were randomly placed in each stand with 70 quadrates in the 19 year old stand, 46 in the 16 year old and 40 in the 13 year old stand and unmined stand.

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[2] Present address: School of Botany and Zoology, University of Natal, P. O. Box X01, Pietermaritzburg, 3209

DATA ANALYSIS

The relationship between abundance and incidence

For rodents minimum number alive (MNA) was calculated for each species in each grid. MNA is simply a count of all the individuals of a species captured on a grid (Krebs 1999). Abundance of millipedes and trees was measured as the number of individuals of each species per quadrat. Incidence was measured as the number of grids or quadrats occupied by a species in a stand. The average abundance, standard deviation and variance of each millipede and tree species was calculated for each different aged stand. These statistics were only calculated for quadrats occupied by a species. Calculating average abundance for all quadrats sampled would result in lowering the abundance of species that occurred in only a few quadrats, which could in turn result in recording an artificial positive relationship between abundance and quadrat occupation (Gaston 1996a, Collins & Glenn 1997, Van Rensbug *et al.* in press). Incidence was expressed as proportional incidence.

Ordinary least squares (OLS) regression analysis was used to test whether a relationship between abundance and incidence existed. Although the assumptions of OLS are often violated when testing for abundance-distribution relationships, it is the most commonly used method (Blackburn and Gaston 1998). Least squares regression analysis assumes normality, homogeneity of variances as well as no error variance in the independent (*X*) variable (Zar 1996), the latter being one of the most commonly violated assumptions (Blackburn & Gaston 1998). Mcardle (1988), however, demonstrated that OLS was an appropriate estimator of the structural relationship when the error variance in the independent variable was about a third of the dependent (*Y*) variable.

In the present study the independent variable (incidence) was reasonably error-free (certainly far lower than that of the dependent variable) as quadrats and grids were randomly placed and quadrat and grid sizes were kept constant throughout the sampling period. Measurement errors were considered negligible as both millipede and tree quadrats were relatively large (210m^2 for millipedes, 256m^2 for trees). A deviation of 20m^2 in quadrat size would result in an error of 9.5% and 7.8% respectively. The inclusion or exclusion of individuals occurring on the border of the quadrats could have resulted in some sampling error. Quadrats were therefore carefully sampled to determine whether individuals were within their borders.

For millipedes further sampling error could have resulted from individuals moving in and out of the quadrat during the sampling period. As millipedes move slowly and did not appear perturbed by surveyors moving through the area, this can also be considered a negligible error. However, millipedes concealed in logs, dense vegetation, leaf litter or below the surface could easily be overlooked. To overcome this, sampling was only conducted from dawn to approximately 10:00 when surface activity is greatest (Van Aarde *et al.* 1996b). For rodents, sampling errors may have occurred through accidental springing of the traps, the use of inappropriate baits and trap-type or trap shyness.

Species sharing common ancestors may flaw interspecific comparisons due to non-independence of data points (Harvey & Pagel 1991). A detailed knowledge of the phylogeny of the three taxa was, however, not available and therefore no analyses to asses the relatedness of species, such as that proposed by Felsenstein (1985), was possible. South African millipede phylogeny is, in fact, currently under revision.

A two-tailed F-test was used to determine if slopes of the OLS analyses deviated significantly from zero. Analysis of covariance (ANCOVA) (Zar 1996) was used to compare the slopes of lines between different stand ages, i.e. whether lines were parallel or not. It was also used to test for differences in line elevations.

The effect of stand age on species abundance and incidence

To determine whether regeneration age had an effect on abundance, the incidence of each species in each stand was grouped into frequency classes. In all stands the number of quadrats sampled were more than ten, allowing proportional frequency classes to be used. The same procedure was followed to determine whether incidence in different aged stands, differed among corresponding abundance frequency classes. Log_{10} transformed abundance was grouped into frequency classes because of the considerable variability in the abundance of species.

The abundance of corresponding incidence or abundance frequency classes were compared using a Kruskall-Wallis non-parametric analysis of variance (ANOVA) (Zar 1996). Where significant differences occurred, Dunn's post-hoc test was used to determine which stands differed from each other.

The effect of stand age on incidence frequency distributions

The incidence frequency distributions of taxa were examined by plotting the number of species occurring in 1,2,3… n quadrats/grids for each taxon. In all cases where the number of sampling sites were more than ten, incidence was expressed as a proportion of the sites occupied.

To test the prediction that species have bimodal incidence frequency distributions, the method of Tokeshi (1992) was followed to quantify modality patterns (see also Collins and Glenn 1997, Van Rensbug *et al.* in press). It is a convenient method of defining and recognising modality patterns in the context of distribution dynamics and takes the number of sites and individuals sampled into account (Tokeshi 1992). The method determines the exact probability of obtaining an observed frequency value (P_c) for the left and right most classes under the null hypothesis of random occurrence of species in a region using the following equation:

$$P_c = \sum_{i=n_l}^{N-n_r} \sum_{j=n_r}^{N-i} \frac{N!h^{i+j}(1-2h)^{N-i-j}}{i!j!(N-i-j)!}$$

where N is the total number of species and h the class interval ($0<h<1$).

$P_c<0.05$ was employed first to separate a significant single/bimodal pattern with respect to the boundary classes (n_l and n_r) from other patterns.

The analyses focused on the left and right most frequency intervals as they can be defined objectively according to the core-satellite species hypothesis of Hanski (1982). Here core refers to the right most frequency class (species occupying > 90% of sites) and satellite to the left most class (species occupying ≤ 10% of sites). The probability of obtaining the observed value of a frequency for the left and right most frequency classes, under the same null hypothesis of random occurrences can be calculated separately as follows:

$$P_l = \sum_{i=n_l}^{N} \binom{N}{i} h^i (1-h)^{N-i}$$

$$P_r = \sum_{i=n_r}^{N} \binom{N}{i} h^i (1-h)^{N-i}$$

For which P_1 = the probability in the left most frequency class, and n_1 = the number of species in the left most frequency class. If $P < 0.05$ for the left and right most frequency class then the distribution is bimodal. Temporal scaling was tested by comparing incidence distributions of taxa between the different aged stands.

Kolmogorov-Smirnov two sample tests (Siegel 1956) were used to compare the frequency distributions of each taxon in the different aged stands. The test assesses the similarity between the underlying distributions of the two samples, by comparing their cumulative distribution functions.

The effect of species dispersal ability on occupancy frequency distributions

The rank-order dispersal ability was assumed to be rodents > millipedes > trees. Occupancy distributions of each taxon within each stand were also compared to each other using Kolmogorov-Smirnov two sample tests.

CHAPTER 4

RESULTS

The relationship between abundance and incidence

The authors and abundance and incidence values of species encountered in this study are listed in Appendix 1, 2 and 3. Only three rodent species were trapped (Table 1), whilst two shrew species were caught coincidentally. *Saccostomus campestris* (pouched mouse) was the most abundant in the 16 year old stand, but exhibited the lowest abundance in the 13 year old stand (Table 1). In addition its incidence was the highest of any species in all the stands, except for the 19 year old stand for which it showed the same incidence as *Mastomys natalensis* (Natal multimammate mouse). *Mastomys natalensis* attained its highest incidence and abundance in the 19 year old stand, but was not found in the unmined stand. A single individual of *Myosorex varius* (dark footed forest shrew) and three individuals of *M. cafer* (forest shrew) were trapped in the 19 year and 16 year old stand respectively. The only other species recorded was *Graphiurus murinus* (woodland dormouse) in the unmined stand, though only three individuals were captured (Table 1).

Table 1. Minimum number alive (MNA) of six sampled grids, median of MNA (*M*) and incidence of rodents and shrews in regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal.

Stand age (years)	Species	MNA on each of the trapping grids						*M*	Incidence
		1	2	3	4	5	6		
13	*Mastomys natalensis*		1					1.0	1
	Saccostomus campestris	3			4	3	3	3.0	4
16	*Mastomys natalensis*			1				1.0	1
	Saccostomus campestris	8	11	11	5	3	4	6.5	6
	Myosorex cafer		1					1.0	1
19	*Mastomys natalensis*		1	4	2	1	1	1.0	5
	Saccostomus campestris	10	12	9		7	7	9.0	5
	Myosorex cafer			1	1			1.0	2
	Myosorex varius	1						1.0	1
Unmined (>60)	*Saccostomus campestris*		1		14	6	21	10.0	4
	Graphiurus murinus	1	1	1				1.0	3

Due to the small sample size, no sensible analyses could be done on the rodent data. However, *Saccostomus campestris* had the highest incidence in all the stands as well as the highest minimum number alive (MNA) values, whereas species occupying less grids, had lower MNA values (Table 1). This suggests that there was an underlying positive relationship between abundance and incidence for rodents.

Neither the tree nor millipede data sets showed homogeneity of variances or normality. Data were therefore $\log_{10}$ transformed. Heterogeneity of variances were reduced, but neither normality nor homogeneity of variances were obtained. Based on OLS, a positive relationship existed between average abundance ($\log_{10}$ transformed) and incidence (expressed as proportional quadrat occupation) for tree and millipede assemblages in all the sampled stands (Table 2). All regression slopes were significantly positive, except for millipedes in the 13 year old stand (Table 2). The prediction of a positive relationship between incidence and abundance was therefore met.

Table 2. Results of ordinary least squares regression between $\log_{10}$ transformed average abundance and incidence for millipedes and trees in regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal. Two-tailed F-tests were used to test if slopes deviated significantly from zero.

Stand age (years)	**r^2**	**Slope ±S.E.**	**F**	**P**
Millipedes				
13	0.33	1.22 ± 0.61	3.99	0.102
16	0.68	1.22 ± 0.36	11.49	0.02*
19	0.87	1.51 ± 0.19	62.29	0.0003*
Unmined (> 60)	0.76	0.95 ± 0.19	36.37	< 0.0001*
Trees				
13	0.80	1.31 ± 0.16	70.03	< 0.0001*
16	0.55	0.66 ± 0.11	37.28	< 0.0001*
19	0.60	0.56 ± 0.07	60.44	< 0.0001*
Unmined (> 60)	0.43	0.30 ± 0.06	39.72	< 0.0001*

*Slope deviates significantly from zero

For millipedes in the regenerating stands, r^2 values increased with stand age but decreased again in the unmined stand (Table 2). The slopes describing the incidence-abundance relationship for millipedes did not follow the prediction of a decrease in slope with an increase in stand age. Whilst the 19 year old stand had the highest slope, there were no significant differences between slopes (ANCOVA, F=0.51, p=0.681) or elevations (ANCOVA, F=2.19, p=0.11).

In the rehabilitating stands only two species, *Centrobolus fulgidus* and *C. richardii*, occurred in more than 80% of quadrats (Figure 9). *Centrobolus fulgidus* was also the most common species in the unmined site in which, *C. richardii* only occupied 67% of quadrats. The *Doratogonus* sp. was the second most common species in the unmined site, occurring in 78% of quadrats.

Trees showed no temporal trend with regards to the fit of the linear model, the 13 year stand exhibiting the best fit (Table 2). Trees met the prediction of a decrease in the regression slopes describing the incidence-abundance relationship with an increase in stand age (Table 2). A significant difference existed between slopes (ANCOVA, F=12.50, p<0.001). There was, however, no significant difference between elevations of lines for trees (ANCOVA, F=0.68, p=0.564). The 13 year old stand had a significantly higher slope compared to the other stands (Table 3). There were no significant differences between slopes amongst the other stands.

Table 3. Pair wise comparison of the slopes describing the relationship between average abundance and incidence using t-tests for the tree assemblage in regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal

Stand age	**p-values**		
	13	**16**	**19**
13	-		
16	<0.001*	-	
19	<0.001*	0.412	-
Unmined (> 60)	<0.001*	0.072	0.280

*indicates a significant difference

Acacia karroo showed the highest average abundance and incidence in the regenerating stands (Figure 10). In the 13 and 16 year old stands, no tree species had an incidence of more than 75%. *Brachylaena discolor* occupied 75% of quadrates in the 13 year old stand while the remainder of species had a incidence less than 30%. *Vepris lanceolata* had the second highest incidence in the 16 year old stand, namely 75%, whereas *B. discolor* only attained 65% occupation in this stand age. Even so, these species had a much lower abundance than *A. karroo* (Figure 10). Several species in the 19 year old and unmined stands had incidence values greater than 75% (Figure 10). *B. discolor* had a 90% quadrat occupation in the 19 year old stand though it was absent from the unmined site.

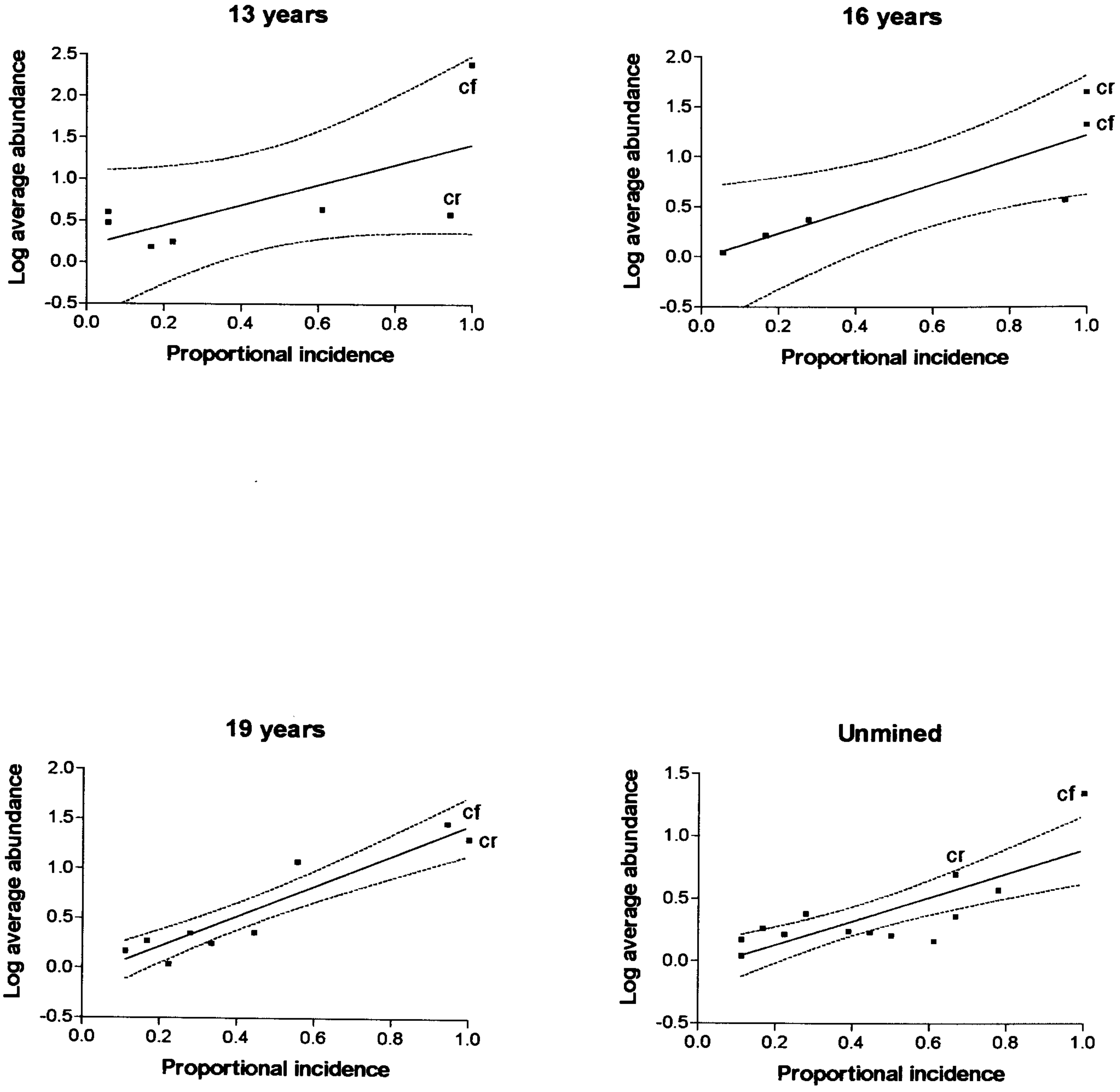

Figure 9. Log_{10} transformed average abundance versus proportional incidence for millipede species on regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal (for r^2 values see Table 2). Dotted lines are 95% confidence intervals of the regression line. cf - *Centrobolus fulgidus*, cr - *C. richardii*.

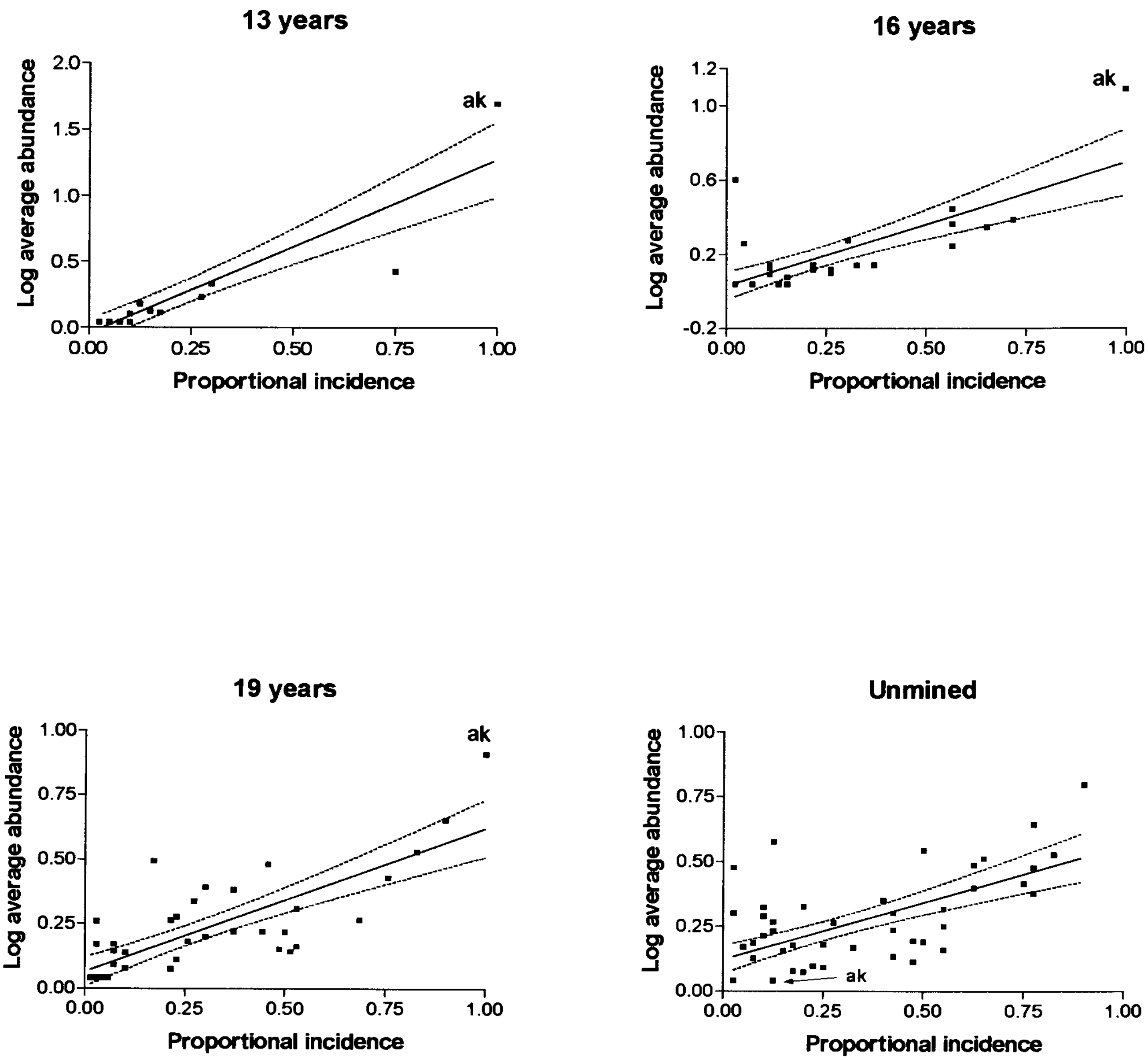

Figure 10. Log_{10} average abundance versus proportional incidence for tree species on regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal (for r^2 values see Table 2). Dotted lines are 95% confidence intervals of the regression line. ak - *Acacia karroo.*

The effect of stand age on species abundance and incidence

No sensible analyses could be performed on the rodent assemblage due to a lack of data. Only the millipede and tree assemblages were analysed to ascertain if there was any temporal effect on abundance and incidence. Several of the frequency classes had no data, therefore only low (≤ 10%), intermediate (50<60%) and high (90-100%) incidence were considered when comparing abundance of millipedes and trees between the different aged stands. The same procedure was followed for abundance, although the values of the frequency classes differed for the different taxa. Abundance and incidence data of the frequency classes did not fit a normal distribution and therefore medians were used to summarise the different frequency classes. In some cases there was insufficient data to calculate the 25th and 75th percentiles (Tables 4-7).

As there were only 15 millipede species in the data, frequency classes often had no data, or only contained data for one species. The millipede assemblage did not follow the prediction that species in the low incidence class would increase in abundance with stand age. Abundance values for the low incidence class peaked in the 13 year old stand (Table 4). Abundance values in the low incidence class differed significantly between stands (KW=7.13, P=0.03), but Dunn's post-hoc test found no difference. *Orthroporoides* sp. and *Centrobolus rugulosus* occupied the 10% class in the 13 year old stand. *Gnomeskelus tuberosus* was the only species with low incidence in the 16 year old stand. Two species, Juliaformia sp. 1 and *Sphaerotherium punctulatum*, occurred in this class in the 19 year old stand. The low incidence class in the unmined stand consisted of the four species *Orthroporoides pyrocephalus*, Juliaformia sp. 1, *Ulodesmus* sp. and *Sphaerotherium* sp.

Table 4. Median abundance (untransformed) and 25th and 75th percentiles of millipede species with low, intermediate and high incidence in regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal.

Stand age (years)	**Median abundance in three incidence classes (low ≤ 10%, intermediate 50<60%, high 90-100%)**								
	Low			**Intermediate**			**High**		
	25th	***M***	**75th**	**25th**	***M***	**75th**	**25th**	***M***	**75th**
13	-	3.5	-	-	-	-	5.0	54.0	240.0
16	-	1.0	-	-	-	-	2.5	16.0	51.5
19	-	1.5	-	7.5	10.5	22.5	12.0	24.0	53.0
Unmined (> 60)	1.0	1.0	1.0	1.0	2.0	1.0	15.0	21.0	36.0

An intermediate incidence of species was only recorded in the 19 year and unmined stands (Table 4). Species in the 19 year old stand obtained significantly higher abundances than the unmined stand (Mann-Whitney U=0.50, P<0.001). Juliaformia sp. 3 occupied the class in the unmined stand and *Spinotarsus* sp. the 19 year stand.

The high incidence class showed no temporal trends with regards to abundance and there was no significant difference between stands (KW=3.58, P=0.31). *Centrobolus fulgidus* had a high incidence in all the sampled areas. This was also the case for *C. richardii* in the regenerating stands, but in the unmined site it only occupied 67% of quadrats. *Spinotarsus* sp. also occupied the high incidence class in the 16 year old stand.

Keeping abundance ($\log_{10}$ transformed) constant for millipedes did not produce clear results. This was as a result of millipedes spanning a very wide range of abundance values, ranging from one to more than 800 individuals per quadrat. The low number of species in the data set also resulted in several of the frequency classes being empty, or having only a single datum point (Table 5).

Table 5. Median proportional incidence (untransformed) and 25th and 75th percentiles of tree species with low, intermediate and high abundance ($\log_{10}$ transformed) in regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal.

Stand age (years)	Median proportional incidence in three abundance classes (low 0.1<0.3, intermediate 1.3<1.5, high 2.3<2.5)								
	Low			Intermediate			High		
	25th	*M*	75th	25th	*M*	75th	25th	*M*	75th
13	-	0.19	-	-	1.0	-	-	1.0	-
16	-	0.17	-	-	0.97	-	-	-	-
19	-	1.4	-	-	1.0	-	-	-	-
Unmined (> 60)	0.19	0.38	0.47	-	-	-	-	-	-

The lowest abundance class had insufficient data, therefore the next class was used for analyses (Table 5). Low abundance species did increase in incidence with age, though the difference between stands was not significant (KW=3.43, P=0.36). *Sphaerotherium giganteum* occupied the low abundance class in the regenerating stands. *Orthroporoides* sp. had a low abundance in the unmined and 19 year stand. In the youngest two stands it occupied the next frequency class. Millipede species therefore changed in abundance and incidence in the different stands.

There was no difference in incidence in the intermediate abundance class and the unmined stand had no species in the intermediate abundance class (Table 5). A single species, in the 13 year stand, namely *C. fulgidus* obtained a high abundance and therefore no analyses were possible.

Tree species with a low incidence in the unmined stand were more abundant than similar species in the regenerating stands (Table 6). The tree assemblage therefore followed the prediction of an increase in abundance with an increase in stand age, with a significant difference between medians (Kruskal-Wallis test; KW=16.5, P<0.05). However, Dunn's post-hoc test, suggested no significant differences between stands.

Bridelia cathartica was the only species with low incidence that occurred in all four stands. *Maytenus mossambicensis* had a low incidence in three stands but it did not occur in the 13 year old stand. Apart from the above species, the species composition of the low incidence class differed markedly between stands. As with millipedes, tree species incidences also changed from one stand to the next and were absent in certain stands.

Table 6. Median abundance (untransformed) and 25th and 75th percentiles of tree species with low, intermediate and high incidence in regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal.

Stand age (years)	**Median abundance in three incidence classes (low ≤ 10%, intermediate 50<60%, high 90-100%)**								
	Low			**Intermediate**			**High**		
	25th	***M***	**75th**	**25th**	***M***	**75th**	**25th**	***M***	**75th**
13	1.0	1.0	1.0	-	-	-	42.5	51.0	59.0
16	1.0	1.0	1.0	1.0	2.0	4.0	9.0	13.0	19.0
19	1.0	1.0	1.0	1.0	1.0	2.0	4.0	7.0	10.0
Unmined (> 60)	1.0	1.0	2.0	1.0	1.0	3.0	4.0	6.0	12.5

Abundances in the intermediate incidence class did not follow any temporal trends (Table 6) though there was a significant difference between stands (KW=11.87, *P*<0.0026). The 13 year old stand had no species in this class, whilst the 16 year old stand had a significantly greater abundance than the 19 year old stand (Dunn's test, P<0.01). The remainder of stands did not differ significantly from each other (Dunn's test, P>0.05). *Allophylus natalensis* had an intermediate incidence in both the regenerating stands, whilst in the unmined stand it had a much lower incidence (only 27.5%). *Sideroxylon inerme* was common to the 19 year old and unmined stands, but only occupied 30.4% of quadrats in the 16 year old stand.

In the high incidence class, abundance decreased with increased stand age (Table 6), following the prediction that species in the high incidence class should decrease in abundance with an increase in stand age. The difference between stands was highly significant (KW=120.5, P<0.001). The 19 year old and unmined stands did not differ significantly in tree abundance (Dunn's test, P>0.05). Tree abundance differed significantly between all other stands (Dunn's test, P<0.05). In the regenerating stands this class consisted of *A. karroo* which occurred in all quadrats. *Brachylaena discolor* attained 90% incidence in the 19 year old stand, whereas *Psychotria capensis* was the only species in this class in the unmined stand and occurred in 90% of quadrats.

Dividing tree abundance into frequency classes and comparing corresponding incidence values did not produce clear results. This was because each abundance frequency class ($\log_{10}$ transformed) covered a wide range of incidence values. As with the millipede assemblage, several of the frequency classes were empty or had too few data to calculate 25th and 75th percentiles (Table 7).

Incidence did not change significantly in the lowest abundance class between stands (Table 7; KW=0.21, P=0.98). The 16-year stand had the highest incidence in the intermediate abundance class (Table 7), but did not differ significantly from the other stands (KW=3.60, P=0.33). The unmined stand had no species in the highest abundance class, whereas the rehabilitating stands had a single species namely, *A. karroo*, recorded at 100% incidence. Tree species with similar abundance therefore did not change significantly with regards incidence across the different aged stands and the prediction of an increase in incidence with an increase in stand age was therefore not met.

The effect of stand age on incidence frequency distributions

Small mammal sampling did not yield sufficient data for analyses. Millipede frequency distributions in the 13 year stand exhibited modes in the lowest (satellite) and highest (core) frequency classes (Figure 11), but showed no significant modality (Table 8). Frequency distributions in the 16 year old stand was unimodal (Table 8), with the mode occurring in the highest frequency class (Figure 11). On the other hand the 19 year stand exhibited a mode in the second lowest frequency class (Figure 11), but showed no significant modality (Table 8). The unmined stand had modes in the second lowest and the fourth highest frequency classes (Figure 11).

Although all the stands showed distinct modes (Figure 11), the lack of any significant P_c values for three of the stands (Table 9) results from the low numbers of species in the millipede assemblage (Table 9). The 13 year old stand exhibited very distinct core and satellite modes (Figure 11), but the modes only differed by one increment from the intermediate frequency classes.

Tree frequency distributions in all the stands were right-skewed (Figure 12) and were significantly unimodal (Table 8). The prediction that younger stands should display a bimodal distribution was therefore not met.

Table 7. Median proportional incidence and 25th and 75th percentiles of tree species with low, intermediate and high abundance ($\log_{10}$ transformed) in regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal.

Stand age (years)	**Median proportional incidence in three abundance classes (low ≤ 0.08, intermediate 0.32<0.40, high >0.8)**								
	Low			**Intermediate**			**High**		
	25th	***M***	**75th**	**25th**	***M***	**75th**	**25th**	***M***	**75th**
13	0.025	0.038	0.5	-	0.3	-	-	1.0	-
16	0.022	0.07	0.1	-	0.65	-	-	1.0	-
19	0.03	0.04	0.06	-	0.3	-	-	1.0	-
Unmined (> 60)	0.03	0.04	0.08	-	0.4	-	-	-	-

Table 8. Classification of incidence frequency distribution patterns of millipedes and trees on regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal based on Tokeshi (1992). P_c = overall distribution, P_l = left most mode, P_r = right most mode.

Stand age (years)	P_c	P_l	P_r	**Diagnosis**
Millipedes				
13	>0.05	>0.05	>0.05	Uniform/other
16	<0.005	>0.05	>0.05	Unimodal
19	>0.05	>0.05	>0.05	Uniform/other
Unmined (> 60)	>0.05	>0.05	>0.05	Uniform/other
Trees				
13	<0.0001	<0.0001	>0.05	Unimodal
16	<0.0001	<0.0001	>0.05	Unimodal
19	<0.0001	<0.0001	>0.05	Unimodal
Unmined (> 60)	<0.0001	<0.0001	>0.05	Unimodal

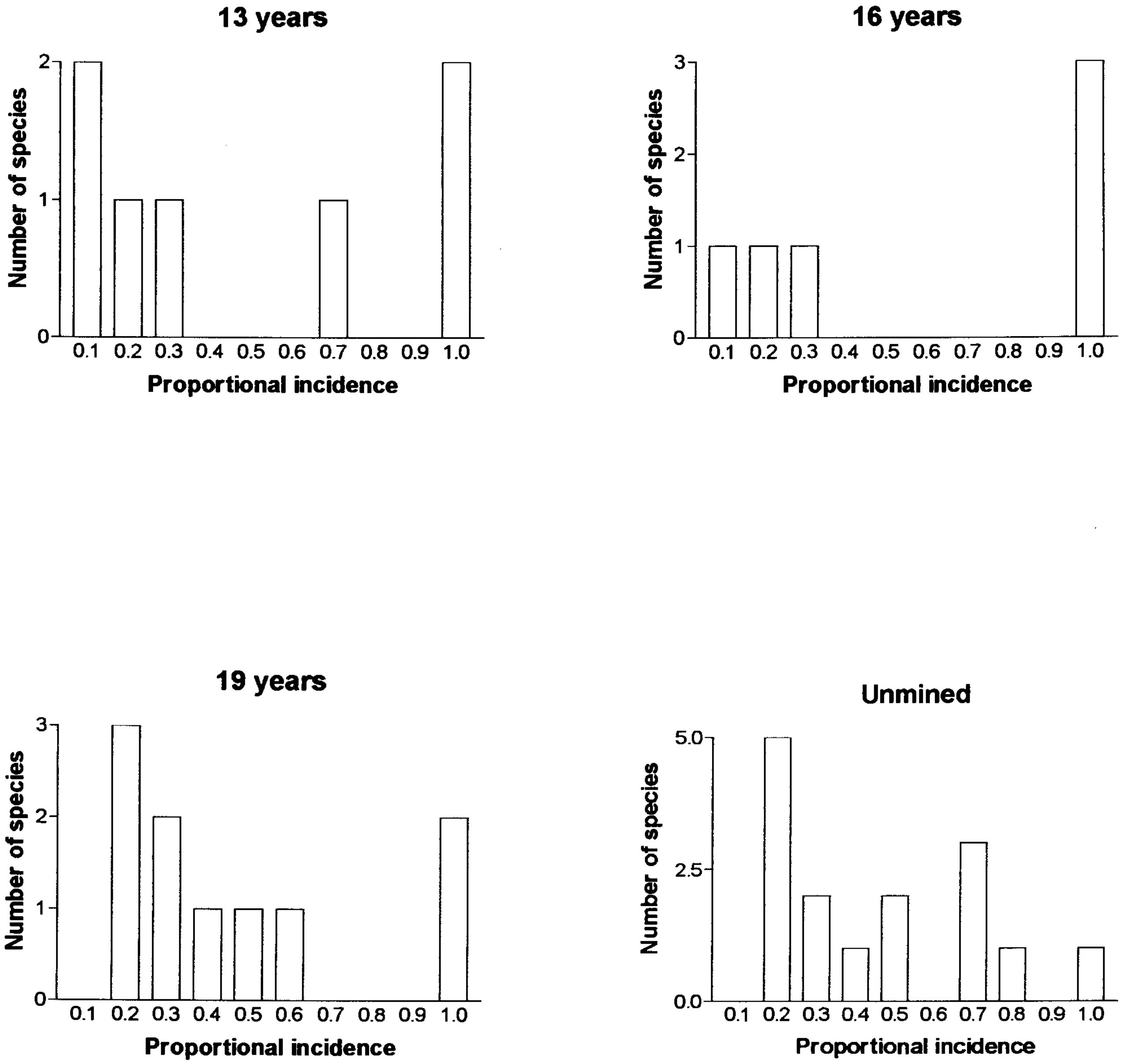

Figure 11. Incidence frequency distributions of millipedes on regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal.

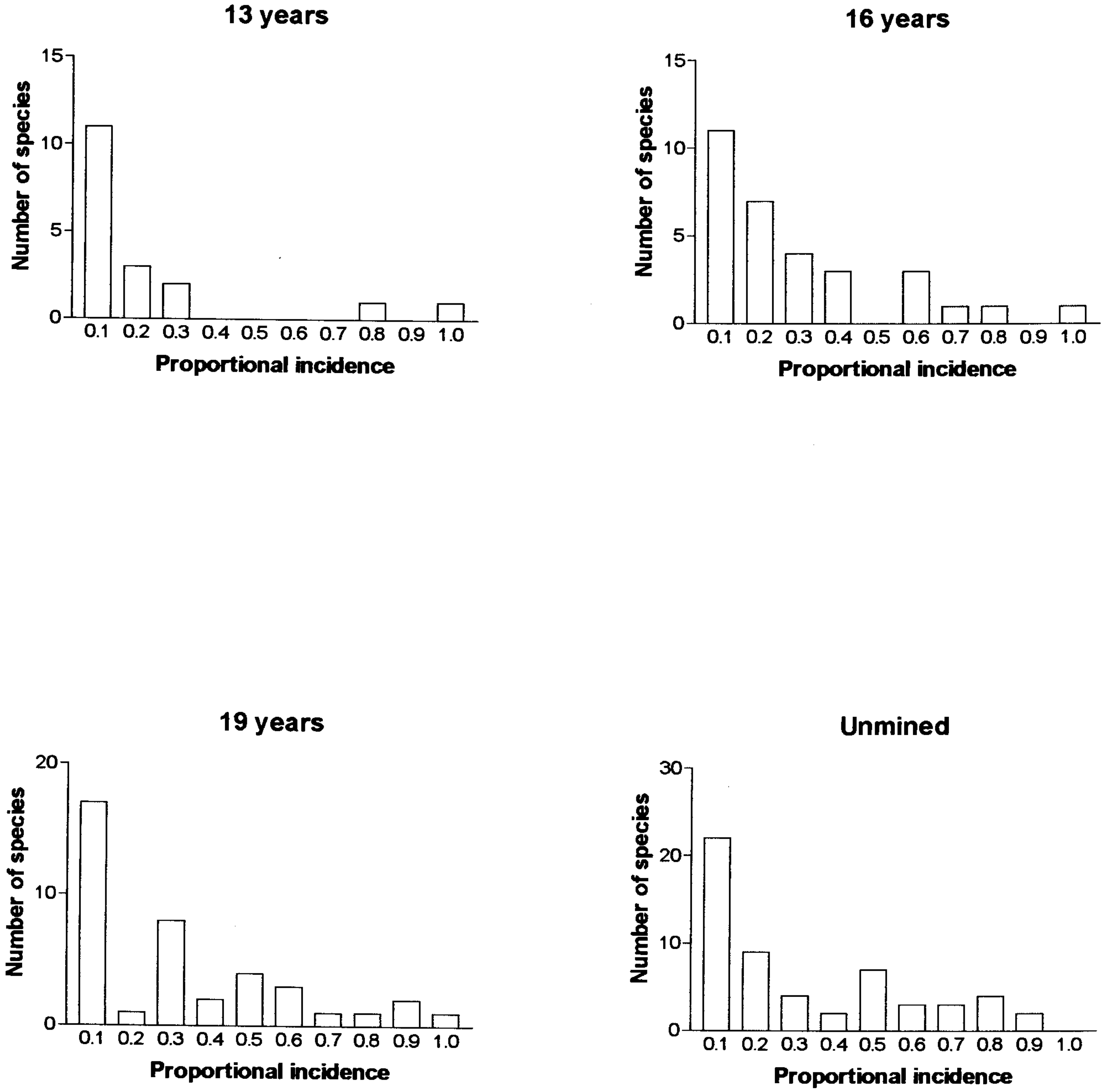

Figure 12. Incidence frequency distributions of trees on regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal.

Millipede assemblages of the different aged stands differed markedly in the percentage of species in the satellite as well as core classes (Table 9). The percentage of satellite species decreased from the youngest to the oldest stand, for which both the 19 year old and unmined stands had no species in the satellite mode. Therefore, millipedes showed evidence of temporal scaling. There was no chronological trend with regards to core species where the 16 year stand had the highest percentage of species (Table 9). Despite differences in the percentage of species in the above-mentioned classes, no significant differences in the underlying frequency distributions of the different aged stands was observed(Table 10).

Table 9. Percentage of species in the satellite (occupying ≤ 10% of quadrats) and core (occupying > 90% of quadrats) modes for millipedes and trees on regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal.

Stand age (years)	Number of species	% Satellite species	% Core species
Millipedes			
13	7	29	29
16	6	17	50
19	10	0	20
Unmined (>60)	15	0	7
Trees			
13	18	61	6
16	31	36	3
19	40	42	3
Unmined (>60)	56	39	0

With regard to temporal scaling, trees did not exhibit any clear pattern. The percentage of satellite species was greatest in the 13 year old stand, but lowest in the 16-year stand (Table 9). The unmined stand did, however, contain a lower percentage satellite species than two of the regenerating stands. The percentage of core species decreased with an increase in age and the unmined stand had no species in the core mode. There were no significant differences in the underlying frequency distributions between stands (Table 10).

Table 10. Within taxon comparison of incidence frequency distributions, using Kolmogorov-Smirnov two sample test, of millipedes and trees on regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal.

Stand age (years)	**p-values**		
	13	**16**	**19**
Millipedes			
13			
16	0.74		
19	0.51	0.51	
Unmined (>60)	0.46	0.20	0.81
Trees			
13			
16	0.22		
19	0.07	0.55	
Unmined (>60)	0.15	0.43	0.61

The effect of species dispersal ability on occupancy frequency distributions

There was evidence supporting organismal scaling, as millipedes recorded a higher percentage of core species than trees in all stands (Table 9). Underlying frequency distributions of millipedes and trees were only significantly different in the unmined stand (Table 11). Frequency distributions of the two taxa in the regenerating stands were therefore similar, despite large differences in the number of species for each assemblage (Table 9).

Table 11. Between taxon comparison of incidence frequency distributions, using Kolmogorov-Smirnov two sample test, between millipedes and trees on regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal.

Stand age (years)	**p-value**
	Millipedes vs. Trees
13	0.29
16	0.11
19	0.06
Unmined (>60)	0.03*

*indicates a significant difference

CHAPTER 5

DISCUSSION

The relationship between abundance and incidence

The millipede and tree assemblages showed a strong relationship between abundance and incidence with high r^2 values compared to those of other studies reviewed by Gaston (1996a). Even though it could not be rigorously analysed, the rodent data also indicated a positive relationship between incidence and abundance, as the most abundant species *Saccostomus campestris* also exhibited the highest incidence in all sampled stands. The slopes describing the abundance-incidence relationship in the millipede assemblage did not differ significantly between different aged stands. Trees, however, did show a decrease in slope with an increase in stand age. The abundance-incidence patterns found in both assemblages differed from those found by Boeken and Shachak (1998), who studied the dynamics of desert plants over time after disturbance. They found an increase in regression line slope with time after disturbance. This increase was directly attributed to early colonisers, which immediately occupied all sites and then steadily increased in abundance over time, resulting in an up-curving trend in the abundance-incidence relationship. Compared to the study of Boeken and Shachak (1998), the lack of observed change (millipedes), or decrease in slopes (trees) in the present study were probably attributable to the later seral stages of the dune forest successional sere I sampled. For these later seral stages early colonisers will already have started decreasing in abundance. Species at the lower end of the abundance-incidence phase plane had little effect on slopes as neither millipedes nor trees showed any differences in line elevations between different aged stands.

Several mechanisms have been proposed to explain the positive relationship between abundance and incidence, or range size (for a review see Gaston *et al.* 1997a). Two of the mechanisms suggest a positive relationship in the absence of any biological effects. Brown (1984) first suggested that the relationship could occur as the result of rare species being under sampled (or over looked), thus causing an artefactual relationship between incidence and abundance. Sampling in the present study was considered to be intensive enough to eliminate the possibility of the positive relationship being a result of insufficient sampling. Hartley (1998) and Wright (1991) suggested the relationship may be expected by chance, due to the spatial aggregation of individuals. Species in the same assemblage, however, often do not have the same patterns of spatial aggregation (Gaston *et al.* 1998a).

Phylogenetic non-independence (Harvey & Pagel 1991) may have flawed the interspecific relationship in my study, as a detailed knowledge of the phylogeny of the three taxa was not available. In fact, the millipede assemblage is currently under review. However, Gaston *et al.* (1997b) found that the relationship between abundance and incidence remained consistently positive, even after controlling for phylogeny in the British avifauna.

Species tend to differ in their abundance across their geographic range (Hengeveld & Haeck 1982, Brown 1984, Brown *et al.* 1995), with abundance peaking towards its centre. Research into the abundance-incidence relationship on the regional and local scale, such as my study, could therefore produce an artificial positive relationship as a result of certain species being at the centre of their range whilst others are towards the edge (Brown 1984). In their ongoing study of the British avifauna, Gaston *et al.* (1997b) found that range position did not effect the abundance-incidence relationship as such, but rather the position a species occupies on the abundance-incidence phase plane. Range position could therefore be considered to be of little importance in influencing the results of the present study.

Metapopulation dynamics have also been proposed as a contending mechanism and have received some attention in the literature (Hanski 1982, Hanski 1991, Hanski & Gyllenberg 1993, Hanski *et al.* 1993, Maurer 1990). The critical question, however, is whether all the species in a specific assemblage have a metapopulation structure. Despite Hanski (1982) and Hanski *et al.* (1993) proposed models, current evidence suggests that several taxa are not governed by metapopulation dynamics. For instance, Brown (1995) found a similar positive interspecific-abundance relationship on islands, for which metapopulation dynamics could be excluded due to the very low rate of over-water dispersal. One of the assumptions of the metapopulation models of Hanski (1982, 1991), Hanski *et al.* (1993) and Nee *et al.* (1991) are that patches are equal, that is all species have the capacity to occupy all patches. This scenario seems highly unlikely in the different aged stands at Richards Bay, for which stands differ in several environmental factors including temperature, humidity, light and soil nutrient levels (Van Aarde 1997, Van Aarde *et al.* 1998). In addition, incidence-frequency distributions of millipedes and trees were not bimodal, further evidence that the observed patterns were not governed by Hanski's (1982) model.

The vital rates hypothesis (Holt *et al.* 1997) is also based on species population dynamics and proposes that species with the lowest death and/or highest birth rates in a specific region should also be the most abundant and widespread. Although it is a very elegant hypothesis, it is difficult to test as it requires very high resolution data of entire assemblages. In addition, the hypothesis is based on density-independent population dynamics. In one test of the vital rates hypothesis, low incidence species in the Negev Desert were site-limited and therefore had density-dependent population dynamics, nullifying this hypothesis (Boeken & Shachak 1998).

Three of the mechanisms discussed by Gaston *et al.* (1997a), namely the resource breadth (Brown 1984), habitat selection (Brown 1995) and the resource availability hypotheses (Hanski *et al.* 1993, Gaston 1994) are strong contenders for explaining the findings of the present study. So too is the habitat availability hypothesis of Venier and Fahrig (1996). The first two can be considered species orientated, where as the latter two can be considered environment orientated. Brown's two hypotheses are very similar, with only a slight change in emphasis from resource use to habitat use. Thus, for all practical purposes they may be considered as a single hypothesis. Habitat selection incorporates resource selection or breadth of resource use; that is species will only select habitats in which they can find sufficient resources. Brown proposes that species that are widespread and abundant should have broad niches i.e. they should be able to utilise a wide variety of resources. In addition they should also show density dependent habitat selection, such that the more a species density increases the more habitats it will occur in. There is little evidence for either of these predictions (Gaston *et al.* 1997a, Gregory & Gaston 2000). On the contrary, it is highly plausible that certain species that utilise a few widely distributed resources be widely distributed and abundant.

The resource and habitat availability hypotheses make no assumptions about niche breadths, which are often very difficult to measure. As with the first mentioned hypotheses, resource availability is merely a subset of habitat availability. Gregory & Gaston (2000) found strong evidence that resource availability was responsible for the positive abundance-range size relationship in the British avifauna. The hypothesis is also the most parsimonious as it is not dependent on any assumptions with regard to niches or population dynamics. Here Gregory & Gaston (2000) used resource in it's broadest sense, i.e. the number of different vegetation/habitat types bird species utilised. Such a broad classification therefore includes forage and nesting site availability as well incorporating environmental factors that species require for survival. For the remainder of the discussion resource and habitat will be used in the same context.

Although the data available for the millipede and tree assemblages do not allow for rigorous testing of any of the above mechanisms, the resource or habitat availability hypotheses seem the most plausible. Metapopulation dynamics and vital rates (Holt *et al.* 1997) should not, however, be completely disregarded as they may also be contributing factors. As mentioned previously, not all species show metapopulation dynamics, but where these do exist, both metapopulation dynamics and vital rates will be directly effected by resource availability. If colonisers of a specific site are unable to obtain sufficient resources they will go extinct. Birth and death rates will be directly effected by the ability of individuals in an area to acquire the necessary resources for survival and reproduction.

Abundant and widespread species in both taxa (as well as the rodent *S. campestris*) probably utilise resources that are widely distributed throughout the successional sere. The lack of key resources from the regenerating stands, probably explains the absence of late successional millipede species such as *Orthroporoides pyrocephalus* and *Ulodesmus* sp. from these areas. Poor dispersal ability could also prevent these species from colonising regenerating stands given that the unmined stand is some distance away. Three millipede species (*Doratogonus* sp., Juliaformia sp. 1 and sp. 3) were absent from the 13 and 16 year old stands, but present in the 19 year old stand, which are in very close proximity of each other, ruling out poor dispersal ability as a limiting factor for these species. The 16 year old stand borders the 19-year stand in places, making the chances of colonists arriving in either of the stands equally probable. In this case, the lack of key resources or adverse environmental conditions in the 13 and 16 year old stands could be the main reason for their absence. Greyling *et al.* (in press) found that millipede behaviour on coastal dune forests was sensitive to relative humidity and that activity was greatest in the early morning when humidity was highest. There is evidence that younger aged stands have lower relative humidity levels than older stands (Van Aarde 1997). The dominance of *C. fulgidus* across the successional sere may be due to this species capacity to tolerate lower humidity levels than other species. Relative humidity might also be the factor restricting *Doratogonus* sp. and Juliaformia spp. 1 and 3 from colonising the 13 and 16 year old stands.

Centrobolus fulgidus, declined in abundance with an increase in stand age, suggesting that more than one factor controls millipede abundance and distribution. If *C. fulgidus* was insensitive to humidity it is anticipated that its numbers would remain reasonably constant, irrespective of stand age. The reasons for the decline in abundance can only be speculated at.

Acacia karroo moved dramatically down the regression slope from the regenerating stands to the unmined stand. This was also the case for *Brachylaena discolor* that was not found in the unmined stand. As the unmined stand is not near the edges of the ranges of the above mentioned species (Pooley 1993), a range position effect (Brown 1984) is probably not responsible for the decline in abundance and incidence of these species. Abundant and widespread tree species in the regenerating stands probably utilise resources that are locally abundant, but which become limited in the unmined forest. Another possibility is that *A. karroo* and *B. discolor* are amongst the few tree species that can tolerate conditions in the early stands as also *C. fulgidus*. Boeken and Shachak (1998) found that low soil moisture levels did not limit species at the top of the abundance-incidence phase plane, where as rare species were restricted to sites with sufficient moisture. In this case, pioneer species would not be utilising widespread resources that other species could not, but surviving without a key resource limiting other species.

The positive abundance-incidence relationship can result from several factors. Identifying the principal mechanisms is problematic (Warren & Gaston 1997). For instance, the evolutionary history of a taxon adds to the variance around the relationship as ancient species have a negative relationship between abundance and incidence due to differential extinction (Johnson 1998). Ancient species limit the risk of extinction by either increasing in abundance or range size. It is not known what effect evolutionary history may have had on the present study.

The resource availability (Gaston *et al.* 1997a) and habitat availability (Venier & Fahrig 1996) hypotheses seem most applicable, chiefly as they are general and widely applicable. Suitable resources and habitat will directly or indirectly affect the establishment and population dynamics of species. In short, the abundance-incidence relationship represents the dynamics of an assemblage (Boeken & Shachak 1998). The position, or absence, of a species on the abundance-incidence relationship in any given area can be influenced by several external factors apart from intrinsic factors such as dispersal ability and resource use. In my study area the rehabilitation process may be important. Areas from where topsoil was collected have varying disturbance histories and the topsoil is also stored for different time periods until the rehabilitation process is initiated (Denton[3] pers. com.). For trees, the species composition of the seed bank in the topsoil could be a contributing factor, not by affecting the shape of the abundance-incidence relationship, but rather the slope and the position of species on the slope.

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[3] Andrew Denton, Richards Bay Minerals, P.O. Box 401, Richards Bay, 3900.

In the regenerating stands *A. karroo* determined the incline of the abundance-incidence slope. As this species is present from as early as one year after rehabilitation (Van Dyk 1997), the amount of seeds in the topsoil could affect its abundance and incidence. Whether the topsoil effects the majority of tree species' abundance and incidence is debatable. Other tree species only start appearing after about ten years (Van Dyk 1997). Therefore we must ask whether the majority of dune-forest species will have viable seeds remaining in the topsoil after 10 years? If this is not the case, then dispersal from remaining forest patches will be the most important factor governing the presence of later successional tree species in regenerating stands. Propagules arriving during the early stages of succession are presumably not successful due to adverse environmental conditions or strong competition from very dense populations of *A. karroo*. Dispersal to younger stands could also be limited if dispersal agents such as birds are avoiding these areas.

Factors affecting the colonisation of sites may influence the abundance-incidence relationship. The distance from source areas can influence the chances of a species colonising an area, especially millipedes and rodents that are dependent on locomotion for dispersal. Large inhospitable areas between source and potential site could limit such dispersal. The size of a regenerating area will also influence potential colonisation as larger areas represent a potentially larger target for dispersers.

In conclusion, it appears that the positive abundance-incidence relationships, found in this study, may result from multiple factors. Untangling the main mechanisms contributing to this can be problematic (Warren & Gaston 1997). The evolutionary history of taxa may add to the variance around the relationship as ancient species have a negative relationship between abundance and incidence due to differential extinction (Johnson 1998).

The effect of stand age on species abundance and incidence.

By keeping either incidence or abundance constant, the effect of stand age on either of the variables could be assessed. The abundance axis represents the net effect of population growth processes and the incidence axis represents patch or site properties such as environmental conditions, including soil nutrient and moisture levels for plants (Boeken & Shachak 1998) or forage and refuge availability for animals such as millipedes. In short, the abundance axis describes the inherent biological constraints of an assemblage and the incidence axis the environmental constraints (Boeken & Shachak 1998). It must, however, be kept in mind that the two are not mutually exclusive with regards their effects on the dynamics of an assemblage as the physical environment can directly influence population dynamics (Begon *et al.* 1990).

Millipede abundance was affected by stand age, but not in a chronological fashion and results were not always significant. The results did not conform to the prediction that abundance should increase with stand age in the low incidence class. Abundance was lowest in the 16 year old stand for the low and high incidence classes, whilst exhibiting the lowest number of species. Similarly, the high incidence class did not follow the prediction of a decrease in abundance with increased stand age. Time related factors such as a chronological increase in abundance in the low incidence class, or a decline in pioneer species' abundance with age, did not therefore affect millipede abundance. It is possible that for low incidence species, reproductive and recruitment rates were independent of site quality and quantity and that intrinsic biological characteristics appear to determine their abundance. The effect of stand age on the incidence axis may not be very informative for millipedes due to the high variance around the abundance-incidence relationship.

As predicted, tree species abundance in the different incidence classes changed with stand age. For low incidence species, the increase in abundance from the 13 year old to the unmined stand, might not be restricted to a temporal effect, i.e. species have had more time to increase in abundance. The regenerating environment could place more constraints on population growth. If environmental conditions were more favourable in the unmined stand we would expect that high incidence species would attain greater abundances here as well. Abundance in the high incidence class, occupied by *A. karroo* was, however, greatest in the regenerating stands. The population of *A. karroo* is senescent (Van Dyk 1997), and in the future *Psychotria capensis*, the species occupying the high incidence class in the unmined stand, might have a greater abundances than high incidence species in the regenerating stands. Similar to my conclusions for millipedes, the suggested temporal effects on abundance may not control tree abundance.

Tree incidence did not change significantly with stand age, confirming age independent constraints on the incidence axis. Abundant tree and millipede species were not effected as they occupied all, or nearly all, sample sites. Low and intermediate abundance species of both taxa were possibly site-limited. It was not possible to assess whether site limitation was due to environmental factors or poor dispersal and/or establishment ability. Constraints on the incidence axis are important for the regeneration process, especially if this is largely due to poor dispersal and colonisation ability. If the physical environment of the regenerating stands continues to develop towards that of the unmined stands, suitable sites for species that are site limited in the unmined site might become available with time.

Life history constraints of poor dispersers and colonisers might limit their establishment, even if the physical environment of the regenerating stands changes towards that of the unmined stand. Species in both assemblages did not always occupy the same incidence or abundance class through out the successional sere. Similar results were reported by Boeken and Shachak (1998), who found that although some species occupied all sites throughout the study period, they changed in abundance from year to year. In my study, species at the lower and middle section of the abundance-incidence phase plane, also often varied in both incidence and abundance from one stand to the next.

The effect of stand age on incidence frequency distributions

Neither the millipede, nor tree assemblages had bimodal incidence-frequency distributions. Therefore, neither assemblage was governed by metapopulation dynamics, based on the core-satellite hypothesis of Hanski (1982) and Hanski *et al.* (1993), nor the model described by Maurer (1990) based on habitat productivity. This does not discredit metapopulation dynamics as a mechanism producing the frequency distributions observed in this study as the metapopulation models of Levins (1969 in Collins & Glenn (1991)) and Nee *et al.* (1991) do not predict bimodal frequency distributions.

Metapopulation models rely on fragmented habitats (Hanski 1982, Collins & Glenn 1997). Although the regenerating area is separated from the unmined area, the two areas are not actually highly fragmented, casting doubt on the existence of metapopulation dynamics. *Acacia karroo*, which occupied all sample sites in the regenerating stands, can be interpreted as a single population and not a group of metapopulations, whilst the same is true for *C. fulgidus* in the regenerating and unmined areas. Metapopulation dynamics may therefore not apply to all the species in the tree and millipede assemblages, as these may not conform to the definition of a metapopulation.

Collins and Glenn (1990) found that, in the absence of disturbance, dominance increases and species richness decreases in communities dominated by large sessile species. Therefore a core mode should be found in undisturbed communities. In the presence of frequent disturbances, high incidence species are most affected and the core mode shifts to the left (Collins & Glenn 1990). I found no evidence for this pattern in the present study. For both millipedes and trees the percentage of species in the core frequency class was lowest in the unmined area.

This area was the least disturbed of all the stands. Apart from the mining operation, cattle grazing (Wassenaar 1998) also affect the regenerating stands. Although grazing might not directly effect trees, trampling could influence tree seedling survival. Millipedes occupying the herbaceous stratum may also be influenced by the defoliation and trampling.

The lack of significant bimodality can be attributed to various factors. Hanski's (1982) core-satellite hypothesis is a regional based model, which assumes the sampled habitats in the region are relatively similar so that all species in an assemblage have equal chance to occupy all sites. In the present study this assumption was violated as each stand has been treated as a separate community. Due to the complex nature of biological communities, the probability of them converging to a single endpoint is debatable (Maurer 1999). There is also evidence of self-similarity in biological systems and patterns at small spatial scales are often mirrored at larger spatial scales (Collins & Glenn 1990, Harte *et al.* 1999). Thus, it may be expected that different habitats would have similar incidence-frequency distributions as the region. Hanski (1982) does not explicitly define "region" and if the region consists of similar habitats, there is no reason why they can not be seen as one habitat. Following this rationale it would be expected that the different aged stands should also have bimodal frequency distributions, even though they are not regional in their extent. The lack of bimodality emphasises the artefactual nature of core-satellite distributions due to both under sampling and the use of small sampling areas (Nee *et al.* 1991). Van Rensburg *et al.* (in press) found that a change in the core frequency class was responsible for altering frequency distributions from bimodal to unimodal as spatial scale was increased. They also found that the satellite mode remained, further evidence for bimodality being a result of an area effect. Current evidence indicates that range size distributions are right skewed (Gaston *et al.* 1998b, Gaston 1996b) and the majority of species thus have small ranges. As most species have small ranges, an increase in sampling area, is accompanied by a decrease in the number of species found in more than 90% of sites (Van Rensburg *et al.* in press).

Even at the patch level the majority of species remain restricted in incidence (Boeken and Shachak 1998). Right-skewed frequency distributions are pervasive and bimodal patterns the exception (Tokeshi 1992). More insight may be gained by investigating the reasons why the majority of species remain restricted in their incidence, rather than exceptional bimodal patterns. Strong evolutionary forces are preventing the majority of species from becoming widespread and common (Boeken & Shachak 1998).

Evidence from coastal dune forests confirms that most species remain restricted in incidence. Regardless of mechanisms, from a conservation perspective right-skewed incidence and range size frequency distributions have two major implications. First, a large percentage of species might face extinctions as range size is negatively correlated with extinction risk (Gaston 1996b) and second, small, protected areas might be sufficient to protect restricted species (Lawton 1993).

Temporal scaling was evident in the millipede assemblage, for which the percentage satellite species decreased with an increase in stand age. Thus, there was a shift to higher incidence classes with an increase in regeneration age. This occurred to such an extent that in the 19 year old and unmined stands no species were recorded in the satellite mode. For trees the pattern was different, but the unmined stand still had a lower percentage of satellite species compared to the 13 and 19 year old stands. As the underlying frequency distributions did not differ, the results might not be related to dispersal. The stands differed markedly in the number of species present and species in the younger stands carry more weight than those present in the older stands, such that temporal scaling may simply represent a statistical artefact.

The effect of species dispersal ability on occupancy frequency distributions

The assumptions of Collins and Glenn (1997) that changes in incidence-frequency distributions between taxa are indications of differences in dispersal ability might not be valid. It is reasonable to assume that at small spatial scales, all species will have had equal opportunities to disperse to all sites over evolutionary time (Van Rensburg *et al.* in press). In snapshot studies incidence frequency distributions might thus not be an indication of dispersal ability, but rather habitat preference and extinction rates within sites (Van Rensburg *et al.* in press). Given the young age of the regenerating stands, however, all species would not have had equal opportunity to occupy all possible sites. The larger percentage of core species in the millipede assemblage could thus be taken as an indication of better dispersal ability. However, caution should be taken with this assumption, as the result was similar in the unmined forest, which represents a snapshot situation. The results were most likely a statistical artefact due to the differences in the number of species of the two assemblages.

CHAPTER 6

CONCLUSION

Post mining regenerating stands of coastal dune forests had positive abundance-incidence relationships and incidence frequency distributions, similar to those recorded in an unmined coastal dune forest, for two of the taxa studied. Sufficient data could not be collected from the rodent assemblage for formal analyses to be performed. Inferring the success of the rehabilitation programme from the observed patterns should be done with caution. Several mechanisms have been proposed to explain the positive abundance-incidence relationship. The contribution of each might depend on the particular taxon, temporal and spatial scales studied. Thus, the underlying mechanisms may vary for each particular stand, as well as the different taxa selected. Separate mechanisms do not necessarily operate from one stand to the next, but rather the relative contribution of each mechanism may differ. I argue that the resource availability hypothesis was the most applicable mechanism, explaining the positive abundance-incidence patterns found in this study. Isolating it from alternative mechanisms proves difficult, as resource availability will affect vital rates and population dynamics in general.

Comparing abundance and incidence separately between stands, no clear temporal trends emerged. I attributed this to the variance around the regression lines that could be fitted to the data. Different abundance-frequency classes often spanned a wide range of incidence intervals. With regard to abundance and incidence, most species were dynamic, and changes in both variables were observed between different aged stands. These changes were not necessarily linear.

Incidence-frequency distributions indicated that Hanski's (1982) core-satellite hypothesis was not responsible for the positive abundance-incidence relationship, as no bimodality was found. The changes in the percentage species in the lowest (satellite) frequency classes of stands suggest temporal scaling. This pattern could result from greater time available for dispersal, but should be interpreted with caution because the number of species differed between stands and therefore species carry more weight in less speciose stands.

The same is true at an organismal scaling level, for which millipedes had a greater percentage core species than trees. Again, this should not be taken at face value as an indication of higher taxon dispersal ability, but rather due to large differences in the number of species between taxa. When making assumptions about temporal and organismal scaling this should be taken into account. Alternatively, assemblages with a similar number of species should be selected.

The study validated the robustness of the positive abundance-incidence relationship and right-skewed incidence frequency distributions. A positive regression slope between abundance and incidence was found even in young, regenerating areas for two taxa and I argued that even at the small spatial scale of this study, the pattern was real and not artefactual. My study also confirmed the double jeopardy faced by rare species (Gaston 1998), namely they are limited in numbers and occurrence. By plotting abundance against incidence the rare species in an assemblage can be identified. Rarity could be a result of inherent biological constraints on population growth rates, poor dispersal, and/or establishment ability (Kunin & Gaston 1993). Poor dispersal ability can be countered by leaving corridors between regenerating and unmined areas. Measures to ensure the establishment of species that are rare due to population growth constraints, in the regenerating areas, are more difficult to undertake. If rare species have poor population growth rates and dispersal due to inherent biological traits that are independent of environmental factors, colonisation of new areas would be difficult, even if the environment becomes favourable.

CHAPTER 7

SYNTHESIS

In its simplest sense ecology seeks to understand the temporal and spatial variation in the abundance and distribution of species (Krebs 1999). Ecology is still some way away from explaining these patterns, even after years of intensive study (Gregory & Gaston 2000). Much ecological research has concentrated on the community level, for which general patterns and laws are often obscured by the complex nature of communities (Lawton 1999, Maurer 1999). The most pervasive pattern to emerge in ecology in recent years is the positive abundance-incidence relationship that holds for a wide variety of taxa and spatial scales (Gaston 1996a). By trying to understand the mechanisms governing this pattern we may understand why certain species are locally abundant and widespread whilst the majority remain limited in abundance and restricted in distribution (Gaston *et al.* 1997a).

In the present study I investigated the relationship between abundance and incidence along a successional sere of regenerating coastal dune forests of known age and an unmined forest older than 60 years. Three taxa, namely rodents, millipedes and trees were studied to increase the generality of the investigation. Temporal effects on abundance and incidence were analysed separately by comparing frequency intervals of each variable between stands. Incidence-frequency distributions were examined as they can shed light on the mechanisms generating abundance-incidence relationships and higher taxon dispersal ability. Rodents provided insufficient data for sensible analyses to be performed. In all the stands sampled, millipedes and trees demonstrated a positive relationship between abundance and incidence. The mechanisms underlying this abundance-incidence relationship may vary between different taxa and stands. No clear temporal trends appeared when abundance and incidence were analysed separately, possibly due to large variance around the abundance-incidence relationship. The possibility also exists that rare species were site limited and that any changes observed in abundance and incidence were, maybe independent of regeneration age. Inherent life history constraints could govern rare species abundance and incidence.

The absence of bimodal incidence-frequency distributions indicated that these taxa were not governed by Hanski's (1982) metapopulation model, nor Maurer's (1990) habitat productivity model. For both millipedes and trees the 13 year old stand had the highest percentage of species in the satellite mode (occupying ≤ 10% of quadrats). This suggested temporal scaling, that is as stand age increases there will be less species with low incidence due to increased time available for dispersal. The large differences in species numbers between stands, however, could make this assumption erroneous.

Following a similar rationale, a greater percentage of core species (occupying > 90% of quadrats) in the millipede assemblage were thought to indicate greater dispersal ability, but here also the same problem of differences in species numbers should be taken into consideration.

Most abundance-incidence patterns have been studied at the macroscopic level, covering the entire ranges of the species in the assemblage. It has been argued that the pattern is artefactual at smaller spatial scales due to a range-position effect (Brown 1984) and the validity of the present study, conducted over an area of approximately 135 ha may be questionable. However, Gaston *et al.* (1997a) found that range position only alters the position occupied by a given species on the regression slope, and not the positive relationship as such. Resource availability is the most parsimonious explanation for the positive abundance-incidence relationship found for millipedes and trees. Only Hanski's (1982) core-satellite hypothesis and Maurer's (1990) habitat productivity hypothesis could be rejected, as incidence-frequency distributions were not bimodal. Metapopulation dynamics could apply, as not all metapopulation models produce bimodal distributions (Nee at al. 1991). I did not, however, consider metapopulation dynamics as the key mechanism responsible for the observed patterns. High incidence species could not be considered as metapopulations as they do not consist of fragmented populations (Hanski 1982), but rather exist as single populations.

Analysing abundance and incidence separately did not produce linear age related results, as the variance around the abundance-incidence regression lines was often high. Possible differences in the initial seed bank of the regenerating stands may also have affected tree abundance and incidence. Further, the distance from source areas differ for the different regenerating stands and this may also affect species abundance and incidence.

Shortcomings of the present study and suggestions for further study

The areas sampled had very low rodent and shrew species richness (only five species), and barred this assemblage from any sensible analyses in a study of this nature. For instance, only two rodent species were trapped in some areas, such as the unmined stand. Lumping data from all stands together, to increase species numbers, would not allow analyses of temporal changes in abundance-incidence relationships and incidence frequency distributions. Even the millipedes were represented by very few species in the youngest two stands, resulting in problems when abundance and incidence was examined separately, as well as with incidence-frequency distributions, where several of the class intervals were empty. This shortcoming meant that the incidence-frequency distributions could not be tested for non-randomness.

In a future study of this nature, more specious taxa should be considered, for example other plant assemblages, insects or arachnids. Good data on birds species are available for the study area, but the small size of individual stands limits the number of independent transects to four or less in each stand, thus species incidence is too low to analyse properly. Again, analysing all stands together in order to increase incidence, will eliminate analysing the data for temporal trends. Variance around the abundance-incidence regression lines complicated independent analyses of the two variables.

The main role of analysing incidence-frequency distribution was a rejection of proposed mechanisms governing the positive abundance-incidence relationship. Using these to analyse temporal, spatial and organismal scaling should be done with great caution when there is large differences between the number of species in the areas and taxa examined, as was the case with the present study.

To formally determine the underlying mechanisms governing the positive abundance-incidence relationship on coastal dune forests, any further studies should determine broad resource use of the species studied. This will allow for analyses similar to those performed by Gregory and Gaston (2000), such that it could be formally established to what degree resource availability contributes to the positive abundance-incidence relationship. Obtaining data on population dynamics to determine the existence of metapopulation dynamics is difficult, especially for speciose taxa. It may be more sensible, from a rehabilitation and conservation point of view, to try determine the factors limiting rare species. If these constraints can be determined, appropriate management steps can be taken to ensure their persistence in the area.

A problem with the study area at Richards Bay is that there is inevitably pseudo-replication. This, and the fact that space for time substitution is used, limits the generalisations that can be inferred from these findings. The first problem can be addressed by incorporating nearby areas with a similar disturbance regime into studies. The further away these are though, the more different they will be, because of spatial auto-correlation.

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SUMMARY

A growing body of evidence has found a positive relationship between local abundance and spatial distribution and several mechanisms have been proposed to explain this robust pattern. I studied the relationship between abundance and incidence of rodents, millipedes and trees on regenerating and unmined coastal dune forests situated at Richards Bay on the north coast of KwaZulu-Natal. Three stands regenerating after sand mining, and an unmined stand were selected for the study. The regenerating stands were 13, 16 and 19 years and the unmined stand was older than 60 years at the time of the study.

Rodents were sampled on six grids of 7×7 Sherman live traps per stand for three trap nights. All captured animals were toe clipped and identified to species level. Abundance was measured as the minimum number alive per grid and incidence as the number of grids per stand a species occupied. Millipedes and trees were sampled using randomly placed quadrats and abundance was measured as the number of individuals of a species per quadrat. Incidence was again measured as the number of quadrats a species occupied in a stand. The average abundance for each species was calculated for occupied quadrats or grids only and incidence was expressed as proportional quadrat/grid occupation. Ordinary least squares regression was used to test whether a structural relationship existed between average abundance ($\log_{10}$ transformed) and proportional incidence. Analysis of covariance was employed to test for differences in slopes and elevations of regression lines between different stands.

Rodent data could not be analysed, as it violated the appropriate statistical limitations. Even so, the most abundant rodent, *Saccostomus campestris*, also had the highest incidence in all the stands. Both millipedes and trees had a positive abundance-incidence relationship in all sampled stands. For millipedes there was no change in regression slopes over time, though the regression slope decreased with time for trees. This decrease was attributed to the decline in abundance of *Acacia karroo* that occupied the top end of the slope in the regenerating stands. In the unmined stand, *Acacia karroo* decreased drastically in both abundance and incidence. Species at the lower end of the regression line contributed little to changes in the slope of the abundance-incidence lines, as both assemblages showed no differences between elevations of the regression lines. Species did not always maintain the same position on the regression slope from one stand to the next, but moved up or down the slope or were absent from a stand.

The influence of stand age on abundance and incidence was assessed independently by grouping each variable into frequency intervals. The corresponding variable of similar frequency intervals between stands was compared using Kruskal-Wallis non-parametric ANOVA. Only low, intermediate and high frequency classes were used, as other classes often had no data. For millipede species with low and intermediate incidence, the 13 year old stand had the highest abundance. Millipedes did not change significantly in incidence when the three abundance classes were compared. In the case of the tree assemblage, species with low incidence obtained the highest abundance in the unmined stand. Similarly, when tree abundance was kept constant there were no significant changes in incidence with stand age.

Incidence frequency distributions were tested for bimodality to determine if metapopulation dynamics based on the core-satellite hypothesis (Hanski 1982) were responsible for the abundance-incidence pattern. Temporal scaling was also investigated, specifically whether the percentage satellite species (occupying ≤ 10% quadrates) decreases with stand age, as more time becomes available for restricted species to increase in incidence. Organismal scaling was investigated following the rationale that millipedes are better dispersers than trees and should therefore be represented by a higher percentage of core species (occupying > 90% of quadrates).

Neither of the assemblages showed significant bimodal incidence-frequency distributions, indicating that Hanski's (1982) metapopulation model was not the underlying mechanism generating the positive abundance-incidence patterns. In the millipede assemblage, there was evidence of temporal scaling. For trees the pattern was less clear, although the 13 year old stand had the highest percentage satellite species and the 16 year old stand had the lowest. For both assemblages Kolmogorov-Smirnov two-sample tests indicated no underlying differences in frequency distributions between stands. !n all the stands sampled millipedes exhibited a higher percentage of core species than trees, suggesting they were better dispersers than trees. Even though there were great differences in the percentage satellite and core species within and between taxa, Kolmogorov-Smirnov two-sample tests indicated no differences in underlying frequency distributions, except for millipedes and trees in the unmined stand. Temporal and organismal scaling are probably the result of a statistical artefact, due to large differences in the number of species between stands and taxa.

The positive abundance-incidence relationship was evident even in the youngest stand sampled. The regression slope of the tree assemblage decreased with an increase in stand age, but the relationship did not degenerate. Resource availability was the most likely overriding mechanism producing the positive abundance-incidence relationships, for which species utilising widely distributed and abundant resources should also attain a high abundance and incidence. Several species changed in both abundance and incidence between stands. This indicates possible changes in the resource spectrum within the successional sere. Species changes were not always linear in nature and this is probably related to differences in both the pre-mining history of stands and their distances to source areas. The resource availability hypothesis could, however, mask the influence of other proposed mechanisms such as vital rates (based on species birth and death rates) as the availability of suitable resources and habitat will directly effect the ability of a population to establish itself on a site and increase in numbers.

This study confirms the double jeopardy faced by rare species, they are limited in both abundance and incidence. This rarity could result from inherent biological constraints on population growth, constraints placed on population growth rates by the physical environment or poor dispersal ability. If there is an age-related change in the physical environment, with time some of these constraints might be alleviated. The influence of poor dispersal ability on colonisation of regenerating areas can be negated by maintaining habitat corridors between regenerating and unmined areas.

Appendix 1. Small mammal median abundance (measured as the minimum number alive) and incidence (number of grids occupied) on regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal.

Order and Family	**Species**	**Author**	**Stand age (years)**							
			13		**16**		**19**		**Unmined (> 60)**	
			M	**Incidence**	***M***	**Incidence**	***M***	**Incidence**	***M***	**Incidence**
Order Insectivora										
Family Soricidae	*Myosorex cafer*	Sundevall	-	-	1.00	1.00	1.00	2.00	-	-
	Myosorex varius	Smuts	-	-	-	-	1.00	1.00	-	-
Order Rodentia										
Family Muridae	*Mastomys natalensis*	Smith	1.00	1.00	1.00	1.00	1.00	5.00	-	-
	Saccostomus campestris	Peters	3.00	4.00	6.50	6.00	9.00	5.00	10.00	4.00
Family Gliridae	*Graphiurus murinus*	Desmarest	-	-	-	-	-	-	1.00	3.00

Appendix 2. Millipede species average abundance ($\bar{X}$, untransformed), standard deviation (S. D.) and proportional incidence on regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal.

Order and Family	Species	Author	Stand age (years)											
			13			16s			19			Unmined (> 60)		
			$\bar{X}$	± S.D.	P.I.	$\bar{X}$	± S.D.	P.I.	$\bar{X}$	± S.D.	P.I.	$\bar{X}$	± S.D.	P.I.
Order Juliaformia														
	Juliaformia sp. 1	NM ?	-	-	-	-	-	-	1.50	± 0.71	0.11	1.00	0.00	0.11
	Juliaformia sp. 2	NM ?	-	-	-	-	-	-	-	-	-	2.00	± 1.41	0.39
	Juliaformia sp. 3	NM ?	-	-	-	-	-	-	3.00	± 2.92	0.28	1.67	± 0.71	0.50
Order Polydesmida														
Family Dalodesmidae	*Gnomeskelus tuberosus*	Lawrence	1.67	± 1.15	0.17	1.00	0.00	0.06	1.00	0.00	0.22	2.33	± 2.31	0.17
Family Gomphodesmidae	*Ulodesmus* sp.	NM ?	-	-	-	-	-	-	-	-	-	1.00	0.00	0.11
Order Sphaerotheriida														
Family Sphaerotheriidae	*Sphaerotherium giganteum*	Porat	2.00	± 1.41	0.22	1.67	± 0.58	0.17	2.83	± 4.02	0.33	2.60	± 1.14	0.28
	Sphaerotherium punctulatum	Brandt	-	-	-	-	-	-	1.50	± 0.71	0.11	2.58	± 1.38	0.67
	Sphaerotherium sp.	NM ?	-	-	-	-	-	-	-	-	-	1.00	0.00	0.11
Order Spirobolida														
Family Pachybolidae	*Centrobolus fulgidus*	Lawrence	335.17	± 268.86	1.00	75.78	± 80.89	1.00	72.12	± 109.15	0.94	28.06	± 19.62	1.00
	Centrobolus richardii	Lawrence	4.29	± 2.08	0.94	32.89	± 38.59	1.00	36.00	± 40.65	1.00	7.42	± 6.46	0.67
	Centrobolus rugulosus	Lawrence	3.00	0.00	0.06	-	-	-	-	-	-	2.13	± 2.10	0.44
Order Spirostreptida														
Family Spirostreptidae	*Doratogonus* sp.	NM ?	-	-	-	-	-	-	2.88	± 2.36	0.44	4.64	± 3.05	0.78
	Orthroporoides pyrocephalus	Koch	-	-	-	-	-	-	-	-	-	1.50	± 0.71	0.11
	Orthroporoides sp.	NM ?	4.00	0.00	0.06	2.80	± 1.79	0.28	2.00	± 1.00	0.17	1.73	± 1.79	0.61
Family Odontopygidae	*Spinotarsus* sp.	NM 15855	6.18	± 5.17	0.61	7.35	± 11.45	0.94	15.60	± 11.63	0.56	1.75	± 0.96	0.22

NM – Natal Museum, awaiting identification.

Appendix 3. Tree species average abundance ($\bar{X}$, untransformed), standard deviation (S. D.) and proportional incidence on regenerating and unmined coastal dune forests at Richards Bay, KwaZulu-Natal.

Family	**Species**	**Author**	**Stand age (years)**											
			13			**16**			**19**			**Unmined (> 60)**		
			$\bar{X}$	**± S.D.**	**P.I.**	$\bar{X}$	**± S.D.**	**P.I.**	$\bar{X}$	**± S.D.**	**P.I.**	$\bar{X}$	**± S.D.**	**P.I.**
Anacardiaceae	*Rhus natalensis*	Bernh.	-	-	-	1.40	± 0.89	0.11	1.86	± 1.24	0.50	1.80	± 0.84	0.13
	Rhus nebulosa	Schonl.	1.00	0.00	0.03	1.25	± 0.62	0.26	1.94	± 1.53	0.44	1.00	0.00	0.03
Apocynaceae	*Carissa macrocarpa*	A. D.C.	-	-	-	1.00	0.00	0.02	3.00	± 2.17	0.30	3.03	± 1.90	0.75
Araliaceae	*Schefflera umbellifera*	Baill.	-	-	-	-	-	-	-	-	-	2.00	0.00	0.03
Asteraceae	*Brachylaena discolor*	D. C.	3.53	± 2.74	0.75	2.97	± 2.63	0.65	5.43	± 3.33	0.90	-	-	-
Celastraceae	*Cassine papillosa*	Kuntze	-	-	-	-	-	-	-	-	-	3.40	± 3.64	0.63
	Maytenus cordata	Loes	-	-	-	-	-	-	2.00	± 1.41	0.03	1.00	0.00	0.03
	Maytenus mossambicensis	Blakelock	-	-	-	1.00	0.00	0.02	1.00	0.00	0.06	1.33	± 0.58	0.08
	Maytenus nemorosa	Marais	-	-	-	1.20	± 0.45	0.11	2.25	± 1.61	0.23	1.80	± 1.44	0.50
	Maytenus undata	Blakelock	-	-	-	-	-	-	1.67	± 1.08	0.26	1.50	± 0.84	0.15
Ebenaceae	*Diospyros natalensis*	Brenan	-	-	-	-	-	-	-	-	-	4.04	± 3.35	0.63
	Euclea natalensis	A. D.C.	-	-	-	-	-	-	-	-	-	1.71	± 0.76	0.18
Erythroxylaceae	*Erythroxylum emarginatum*	Thonn.	-	-	-	-	-	-	-	-	-	5.68	± 4.28	0.78
Euphorbiaceae	*Antidesma venosum*	E. Mey.	-	-	-	2.00	± 1.41	0.04	1.00	0.00	0.04	-	-	-
	Bridelia cathartica	Bertol.f.	1.00	0.00	0.10	1.00	0.00	0.07	1.00	0.00	0.03	1.00	0.00	0.03
	Drypetes natalensis	Harv.	-	-	-	-	-	-	-	-	-	1.00	± 0.00	0.03
	Erythrococca berberidea	Prain	-	-	-	-	-	-	-	-	-	2.25	± 0.96	0.10
Flacourtiaceae	*Dovyalis longispina*	Warb.	-	-	-	-	-	-	1.00	0.00	0.03	1.67	± 1.15	0.08
	Dovyalis rhamnoides	Harv.	-	-	-	-	-	-	-	-	-	2.00	± 0.00	0.03
	Kiggelaria africana	L.	-	-	-	1.00	0.00	0.02	1.50	± 0.71	0.03	1.50	± 0.71	0.05
	Scolopia zeyheri	Harv.	-	-	-	-	-	-	-	-	-	1.00	± 0.00	0.03
Icacinaceae	*Apodytes dimidiata*	E. Mey.	1.60	± 0.89	0.13	1.00	0.00	0.13	2.04	± 1.89	0.37	2.75	± 2.31	0.20
Loganiaceae	*Strychnos gerrardii*	N. E. Br.	-	-	-	-	-	-	-	-	-	1.00	± 0.00	0.03
	Strychnos madagascariensis	Poir.	-	-	-	-	-	-	1.00	0.00	0.01	1.94	± 1.20	0.43

Appendix 3 continued on next page.

Appendix 3. Continued

Family	**Species**	**Author**	**Stand age (years)**											
			13			**16**			**19**			**Unmined (> 60)**		
			X̄	**± S.D.**	**P.I.**	**X̄**	**± S.D.**	**P.I.**	**X̄**	**± S.D.**	**P.I.**	**X̄**	**± S.D.**	**P.I.**
Meliaceae	*Ekebergia capensis*	Sparrm.	-	-	-	1.00	0.00	0.07	1.00	0.00	0.06	-	-	-
	Trichilia dregeana	Sond.	-	-	-	1.00	0.00	0.02	1.43	± 0.79	0.10	1.60	± 0.84	0.25
	Trichilia emetica	Vahl.	-	-	-	1.30	± 0.48	0.22	1.31	± 0.70	0.23	2.59	± 2.09	0.55
Mimosaceae	*Acacia karroo*	Hayne	51.08	± 11.66	1.00	14.96	± 8.99	1.00	9.43	± 4.46	1.00	1.00	0.00	0.13
	Albizia adianthifolia	W. F. Wright	-	-	-	4.00	0.00	0.02	1.40	± 0.55	0.07	-	-	-
Myrtaceae	*Eugenia capensis*	Harv.	1.00	0.00	0.03	-	-	-	1.00	0.00	0.03	-	-	-
Ochnaceae	*Ochna arborea*	Burch.	-	-	-	-	-	-	1.14	± 0.38	0.10	2.69	± 1.74	0.40
	Ochna natalitia	Walp.	-	-	-	-	-	-	1.00	0.00	0.01	3.00	0.00	0.03
Oleaceae	*Chionanthus foveolatus*	Stearn	-	-	-	-	-	-	-	-	-	1.68	± 0.95	0.48
	Chionanthus peglerae	Stearn	-	-	-	-	-	-	-	-	-	1.00	0.00	0.03
Rhamnaceae	*Scutia myrtina*	Kurz	1.33	± 0.52	0.15	1.41	± 0.62	0.37	1.50	± 0.90	0.49	1.33	± 0.58	0.08
	Ziziphus mucronata	Willd.	-	-	-	1.40	± 0.55	0.11	1.80	± 1.79	0.07	1.32	± 0.67	0.48
Rubiaceae	*Canthium inerme*	Kuntze	3.00	± 3.02	0.30	2.08	± 1.65	0.57	4.29	± 2.91	0.83	2.14	± 1.70	0.55
	Catunaregam spinosa	Tirvengadum	-	-	-	-	-	-	1.00	0.00	0.04	1.14	± 0.38	0.18
	Kraussia floribunda	Harv.	-	-	-	1.14	± 0.38	0.15	3.38	± 2.80	0.76	6.00	± 7.38	0.13
	Psychotria capensis	Vatke	-	-	-	-	-	-	-	-	-	8.86	± 7.18	0.90
	Psydrax obovata	Bridson	2.00	± 1.73	0.28	1.00	0.00	0.07	3.75	± 2.26	0.17	2.25	± 1.50	0.10
	Tricalysia lanceolata	Burtt Davy	1.00	0.00	0.05	1.50	0.58	0.09	2.10	± 1.36	0.69	2.29	± 1.40	0.43
	Tricalysia sonderiana	Hiern	-	-	-	1.00	0.00	0.04	1.20	± 0.45	0.07	2.00	± 1.00	0.13
	Vangueria sp.		-	-	-	-	-	-	-	-	-	4.31	± 3.34	0.65
Rutaceae	*Clausena anisata*	Willd.	1.00	0.00	0.03	1.47	± 0.92	0.33	3.32	± 4.06	0.27	1.69	± 1.38	0.33
	Teclea gerrardii	Verdoorn	-	-	-	-	-	-	-	-	-	5.36	± 5.78	0.83
	Vepris lanceolata	Lam.	1.29	± 0.49	0.18	2.91	± 1.94	0.72	4.81	± 5.26	0.46	4.45	± 4.97	0.78
	Zanthoxylum capense	Thunb.	-	-	-	1.42	± 1.16	0.26	1.13	± 0.35	0.21	1.75	± 0.96	0.10

Appendix 3 continued on next page.

Appendix 3. Continued.

Family	**Species**	**Author**	**Stand age (years)**											
			13			**16**			**19**			**Unmined (> 60)**		
			X̄	**± S.D.**	**P.I.**	**X̄**	**± S.D.**	**P.I.**	**X̄**	**± S.D.**	**P.I.**	**X̄**	**± S.D.**	**P.I.**
Sapindaceae	*Allophylus natalensis*	De Wint.	1.00	0.00	0.05	3.27	± 3.12	0.57	1.50	± 1.06	0.51	2.18	± 1.78	0.28
	Pancovia golungensis	Exell. & Mendonca 19??	-	-	-	-	-	-	-	-	-	1.00	0.00	0.03
Sapotaceae	*Englerophytum natalense*	Krause	-	-	-	-	-	-	-	-	-	7.40	± 9.79	0.50
	Mimusops caffra	E. Mey.	1.00	0.00	0.03	1.00	0.00	0.07	1.71	± 1.01	0.30	1.22	± 0.44	0.23
	Sideroxylon inerme	L.	-	-	-	2.29	± 2.09	0.30	2.73	± 2.57	0.53	1.50	± 0.74	0.55
Thymelaceae	*Peddiea africana*	Harv.	-	-	-	-	-	-	-	-	-	1.13	± 0.35	0.20
Tiliaceae	*Grewia occidentalis*	L.	1.25	± 0.50	0.10	1.30	± 0.48	0.22	2.07	± 1.33	0.21	2.00	0.00	0.03
Ulmaceae	*Celtis africana*	N.L. Burm.	1.00	0.00	0.08	3.46	± 2.27	0.57	3.96	± 4.49	0.37	3.06	± 2.46	0.78
	Chaetacme aristata	Planch.	-	-	-	-	-	-	-	-	-	1.41	± 0.80	0.43
	Trema orientalis	Bl.	1.00	0.00	0.03	-	-	-	-	-	-	1.50	± 0.71	0.05
Verbenaceae	*Clerodendrum glabrum*	E. Mey.	1.00	0.00	0.05	1.00	0.00	0.15	1.62	± 1.28	0.53	1.20	± 0.42	0.25
	Clerodendrum myricoides	Vatke	-	-	-	-	-	-	1.00	0.00	0.03	1.33	± 0.58	0.08