

RESEARCH ARTICLE

Landscape Composition Influences the Restoration of Subtropical Coastal Dune Forest

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Abstract

Successional processes should increase habitat complexity, and increase resources available for forest-associated species. However, according to the theory of Island Biogeography, the size, amount of edge, and isolation of a habitat patch will influence the probability of successful colonization. If this is true for restoring patches of coastal dune forest, then restoration managers need to mitigate for spatial characteristics.

We used patch occupancy models to assess correlations between the probability of forest birds and trees being present in a patch and patch characteristics that measured age, area, isolation, and the amount of edge. We surveyed birds and trees in an unmined coastal dune forest, remnant patches within the mine lease, and regenerating patches,

some of which were being rehabilitated by a mining company. Contrary to expectations patch age only explained the patch occupancy of 6 of 21 birds and 11 of 25 woody plant species. Landscape spatial parameters, measuring edge, isolation, and area explained the patch occupancy of the remaining 15 birds and 14 woody plant species. However, responses to patch characteristics were varied and idiosyncratic. These varied responses may be related to species habitat affinities, dispersal abilities, and establishment constraints. For restoration to succeed, managers need to consider the spatial configuration of the landscape to facilitate colonization of rehabilitating patches.

Key words: birds, dune forest, mining, patch occupancy, rehabilitation, woody plants.

Introduction

Restoration of the ecological character of disturbed land is a legitimate way of managing a mine's environmental impact (Cooke & Johnson 2002). However, the challenge of doing this successfully, at least in unambiguous ecological terms, remains large. Several factors, ranging from political to climatic, may influence success at restoring ecological structure and function. The relative importance of many of these factors is likely to differ among projects, but some factors may be more general. Here, we are concerned with one such factor that has the potential to be a common determinant in many projects: the landscape and its ecological configuration. The term "landscape" encompasses the structure, composition, and spatial arrangements of habitat patches that may have an ecological influence on the success of a restoration project.

In keeping with the current understanding of ecological concepts, there has been an increasing call to include landscape or spatial components when managing habitat restoration (Huxel & Hastings 1999; Scott et al. 2001; Choi 2004; Miller & Hobbs 2007). Solid theoretical foundations form

the basis of this call—a large part of what we know about how communities are structured rests on ideas about how landscape might influence assembly processes. For instance, Island Biogeography Theory (MacArthur & Wilson 1963) and its subsequent incarnations suggest that patch characteristics, such as the area of a discrete habitat patch, its isolation from other patches, and various properties of its edge influence its species composition and abundance (Brittingham & Temple 1983; Andrén & Angelstam 1988; Saunders et al. 1991).

The importance of the landscape for restoration is perhaps immediately obvious, but the mechanisms that link landscape characteristics to community structure may not be. There may be many such mechanisms, for instance, small habitat patches may have fewer species than large patches, because larger patches are more heterogeneous and therefore have more potential habitats, and consequently more species (Harner & Harper 1976). Also, as the distance between a "mainland" (or a large undisturbed patch) and another patch increases, the probability of successful dispersal from the source patch decreases (MacArthur & Wilson 1963). The relative size of a habitat's edge may influence species persistence through a number of abiotic and biotic interactions between the patch inhabitants and the non-patch matrix. For birds, these include increased nest predation (Andrén & Angelstam 1988) and nest parasitism (Brittingham & Temple 1983). For other taxa, changes in microclimate at the edge of a patch may lead to

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changes in the resources available for a species, or fall outside its climatic threshold (Murcia 1995).

We have been conducting research on post-mining restoration of coastal dune forests in South Africa since 1992 (van Aarde et al. 1996). Restoration here depends on natural colonization of rehabilitating sites from adjacent forested areas (van Aarde et al. 1996). This is ecological recovery sensu MacMahon and Holl (2001). The premise behind this approach is that as a site ages it is exposed to a greater number of potential colonizers dispersing from undisturbed (or minimally disturbed) forests (Wassenaar et al. 2005). This increased diversity presents a greater number of niches and distinct niches for species to utilize, leading to a successional pattern as pioneer species are gradually replaced by species characteristic of mature forests (van Aarde et al. 1996; Kritzing & van Aarde 1998; Wassenaar et al. 2005).

Although the ecological recovery approach has been criticized, as its outcomes can be highly unpredictable (MacMahon & Holl 2001), it is still considered valid restoration practice (Scott et al. 2001; Young et al. 2005; Halle 2007). However, this approach does not provide for spatial limitations that may be imposed by the landscape and assumes an unhindered, unlimited, and stable source of species beyond the areas targeted for recovery through ecological processes.

Our interest in the landscape's potential influence on restoration success stems from land use changes that the study region has experienced since the inception of the rehabilitation program in 1977. Influxes of people stimulated by industrial development, extensive transformation of grasslands and forests to commercial plantations, and the extending reach of mining collectively fragmented the landscape into an unnaturally diverse mosaic of forested patches. A changing landscape might influence restoration through changing dispersal and colonization rates due to changes in the nature of the inter-patch matrix. In addition, a changing landscape may increase the number of sink habitat patches relative to the number of source habitat patches (Keagy et al. 2005).

We are interested in this for practical reasons: if the landscape is a dominant driver of community assembly processes after disturbance, it should form a distinct part of rehabilitation management planning. The relative position of rehabilitating sites to source areas suddenly becomes an important and often manageable factor.

To gauge the influence of landscape on restoration, we assessed the probability of patch occupancy for both forest-associated birds and woody plants as a function of patch area, isolation (a measure of distance), and edge. We further included in to our analysis patch age as earlier studies on species addition and replacement with increasing age point to succession taking place (Wassenaar et al. 2007). We sampled unmined forests as well as forests regenerating along a successional sere imposed by known-age mining and non-mining-related disturbances. We reasoned that if the presence of typical forest species in these patches is strongly related to landscape properties, the likelihood of restoring these species in rehabilitating areas through successional processes alone would be low, unless the landscape itself is managed.

Methods

Study Site

The coastal dune forests north of Richards Bay, KwaZulu-Natal, South Africa, fall within the southern most part of the Maputaland centre of plant endemism (van Wyk & Smith 2001). The climate is humid and subtropical, with mean annual rainfall of 1513 ± 449 mm (mean \pm SD, $n = 32$ years between 1976 and 2008; data courtesy of Richards Bay Minerals). Rainfall peaks in February and during summer the average temperature is 21.5°C (Wassenaar & van Aarde 2002).

The study site included circa 60 km of coastline between Richards Bay Town ($28^{\circ}43'S$, $32^{\circ}12'E$), and the Sokhulu forest ($28^{\circ}27'S$, $32^{\circ}25'E$; see Fig. 1). Dune forest (in its undisturbed state) formed a narrow strip of vegetation along the coast no wider than 1.9 km at its widest point (van Aarde et al. 2004). Within this area, Richards Bay Minerals have been mining for zircon, ilumenite, and rutile since 1976. The dredge-mining process involved the removal of vegetation; the topsoil was collected and stored for use in subsequent dune forest restoration. Post-mining, the sand was re-shaped in to dunes (resembling pre-mining topography) and for indigenous restoration topsoil seeded with annuals was spread over them. From then on restoration relied on the natural successional process (see van Aarde et al. 1996). The pioneer tree species, Sweet thorn (*Acacia karroo*) dominated, to form closed-canopy woodlands. After 12 years, typical mature forest species that have successfully dispersed to the site began to appear, and as it aged the woodland became more similar to a coastal dune forest in terms of species composition and abundance (Wassenaar et al. 2005). Richards Bay Minerals is committed to restoring one-third of its mined area to indigenous coastal dune forest, and the remainder to commercial plantations (van Aarde et al. 1996).

Bird and Woody Plant Surveys

As the target for restoration is an assemblage similar (within natural variation) to that of an unmined coastal dune forest, we limited our analysis of both birds and woody plants to forest-associated species (according to Gibbon (2006) for birds, and Coates-Palgrave (2002) and Pooley (2003), for woody plants). The term forest-associated species is a qualitative judgment of which species are more closely associated with forest (inclusive of forest edge). Species recorded in the Sokhulu forest, and nearby Mapelane Coastal Dune Forest Nature Reserve consistently during our 18 years of fieldwork, were considered forest associated.

Bird surveys took place in January and February 2008 at four different types of patches (Fig. 1). These were "Rehabilitating patches" which were regenerating after mining disturbance (nine sites), "Spontaneous regenerating patches" were regenerating after non-mining-related disturbance (without management intervention; 10 sites). "Forest patches" were remnant forests within the lease that are surrounded by exotic plantations and mining operations (four sites). The "Sokhulu forest" was the largest undisturbed patch of forest in the study

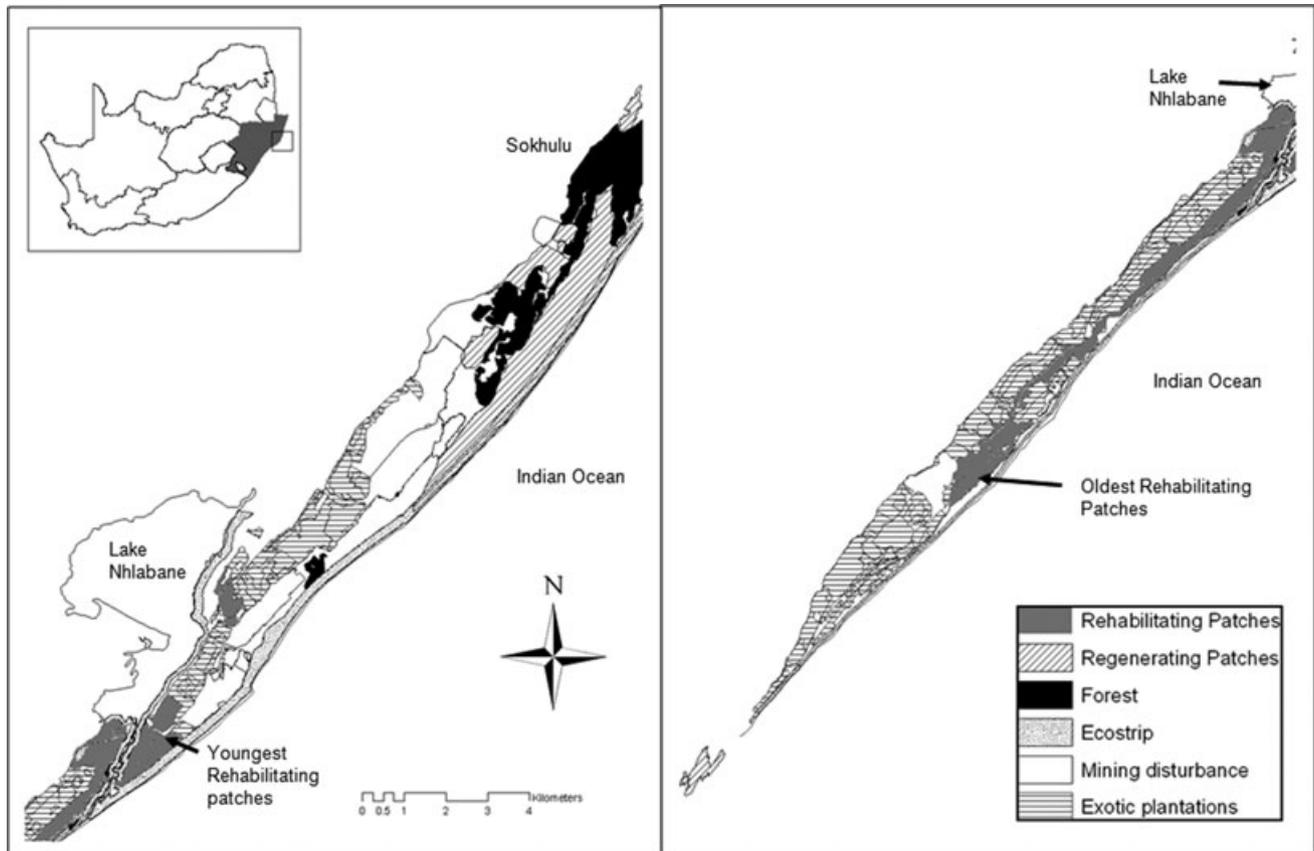


Figure 1. A map of the study area showing in the left hand insert the political map of South Africa, with the province KwaZulu-Natal highlighted, and the study area boxed. In the left panel the northern section of the lease (from Lake Nhlabane to Sokhulu) is displayed showing the Sokhulu forest as well as some of the youngest rehabilitating patches, the majority of spontaneous regenerating patches, and all forest patches. The right panel shows the southern section of the lease (from Lake Nhlabane to Richards Bay Town), showing the older rehabilitating patches and the remaining spontaneous regenerating sites. In-land from the lease the landscape is dominated by human habitation and exotic plantations.

region. Forest patches and spontaneous regenerating patches were located using historical aerial photographs. Patches that had vegetation cover in the earliest set of photographs available for assessment (1937), and were still composed of forest in the 2005 photographs were classified as primary forest patches. Those patches that were bare sand in 1937 but that were covered with vegetation in subsequent images in the time series (1957, 1960, 1970, 1992, 2002, and 2005) were identified as spontaneously regenerating patches of known age.

Rehabilitating patches were defined from mining records; a patch was an area where rehabilitation was initiated within a 4-year-period grouped together as one patch (Wassenaar et al. 2005), and where natural features (such as a river or estuary), exotic plantations, or roads adjoined or surrounded the patch.

For bird surveys, experienced observers walked five 300-m-long line-transects that were separated by 200 m and recorded all birds seen within a distance of 60 m either side of the transect line and all birds heard at each patch. In total data were available for 24 patches.

Woody plant surveys were carried out in 2005 in three types of sites, rehabilitating sites (seven sites), spontaneous regenerating sites (six sites), and the Sokhulu forest. Self-supporting

woody plants greater than 1.7 m in height were identified in seven 16×16 -m quadrats per patch. Woody plant surveys were carried out at rehabilitating patches, spontaneously regenerating patches, and at Sokhulu forest. Data were available for 14 patches.

We assume that in both rehabilitating and spontaneously regenerating coastal dune forest that trees have colonized by dispersal from elsewhere. Dune forest trees generally have recalcitrant seed, meaning that they do not remain viable in topsoil for very long because of desiccation (Nichols 2005). In addition, our previous monitoring and research has only recorded wind dispersed pioneer species occurring in the earliest stages of rehabilitation.

Patch Parameters

For rehabilitating patches, age was determined from mining records. For spontaneously regenerating patches age was determined from digitized georeferenced aerial images of 1937, 1957, 1960, 1970, 1992, 2002, 2005.

Patch isolation from the largest intact forest (Sokhulu forest) was measured in ArcMap version 9.2 (Environmental

Systems Research Institute [ESRI], Redlands, CA, U.S.A.). Distances were taken as edge to edge measurements. The other patch parameters (patch area, and patch shape index) were determined using metrics within the program FRAGSTATS (McGarigal & Marks 1995).

As correlations between patch variables can potentially confound the interpretation of patch occupancy results, we tested for correlation between patch variables using Pearson's correlation coefficient.

Patch Occupancy Probability

We used patch occupancy models in PRESENCE version 2.2 (Hines 2006) to determine if patch parameters (estimated patch age, patch area, distance from the largest forest patch [which in this case was Sokhulu forest], and patch shape index) affected the probability that a patch was occupied by a species. The patch occupancy model assumes (1) that the focal species cannot colonize (or immigrate to) or go locally extinct at a patch during the survey period, (2) species are not falsely detected, and (3) that detection at one patch is independent of detection at other patches (Donovan & Hines 2007).

Patch occupancy models use the logit link and a maximum likelihood approach to estimate ψ , the probability of patch occupancy and p_i , the probability of detecting the species of interest on transect i (given that it is present in the patch) as a function of patch specific covariates. We used the global model: $\psi (P_{\text{age}} + P_{\text{area}} + P_{\text{isolation}} + P_{\text{shape}}) p (T.)$, where $p (T.)$ is the detection probability across all transects (p_1, p_2, p_3, p_4 , etc.) and P denotes the patch characteristics: estimated patch age (P_{age}), patch area (P_{area}), distance from Sokhulu ($P_{\text{isolation}}$) and patch shape index (P_{shape}).

Our candidate model set consisted of the global model and all combinations of patch characteristics. The global model fit was tested using the MacKenzie and Bailey Goodness of Fit test, where the observed data and a simulated dataset are subjected to Pearson's Chi-square tests. If the Chi-square of the observed data divided by the average of the test statistics from 1,000 parametric bootstraps is about 1, the model was considered a "good fit" (MacKenzie et al. 2006). Models were ranked using Akaike's criterion, corrected for small sample size (AICc). However, where over dispersion was detected in the global model ($\hat{c} > 1.0$) the small-sized quasi-AIC (QAIC) was used instead (Burnham & Anderson 2002; MacKenzie et al. 2006). AICc and QAICc are calculated as follows:

$$\begin{aligned} \text{AICc} &= -2 \log \text{Likelihood} + 2K \\ &\quad + 2K(K + 1)/(n - K - 1) \\ \text{QAICc} &= -2 \log \text{Likelihood}/\hat{c} + 2K \\ &\quad + 2K(K + 1)/(n - K - 1) \end{aligned}$$

where K is the number of parameters in the model and n is the effective sample size. The determination of the effective sample size is conceptually difficult in patch occupancy modeling (MacKenzie et al. 2006). We used the number of

sites as our effective sample size ensuring the maximum penalty in AICc and QAICc calculation. AIC values are relative and therefore a more intuitive way to view them is as ΔAIC . This was calculated as $\text{AIC}_i - \text{AIC}_{\text{min}}$, where the best-ranked model is $\Delta\text{AIC} = 0$. These values allowed models to be categorized as having substantial support (< 2), less support ($2 - 7$), and no support (> 10) (Burnham & Anderson 2002). We then calculated Akaike weights (w_i) which approximated the probabilities that model "i" was the best model in the set (Burnham & Anderson 2002). A single model with a weighting greater than 0.9 was considered to be the best model overall. We also calculated the relative variable importance, the sum of all w_i 's of all models in the set containing the variable of interest (Burnham & Anderson 2002).

Results

Patch Characteristics

Rehabilitating patches were more isolated from the largest intact forest, than the spontaneous regenerating patches (with the exception of two). Rehabilitating patches and forest patches had a greater amount of edge when compared with spontaneous regenerating forest patches (Fig. 1). None of the patch characteristics were significantly correlated with each other.

Bird and Woody Plant Surveys

We recorded 39 bird and 36 woody plant forest-associated species. Fourteen of the birds and eight of the woody plants were considered "rare" as they were recorded fewer than four times during the surveys; these species were excluded from further analysis. Models for 25 bird and 28 woody plant species fitted to the observed data.

For 4 of the 25 bird species the probability of patch occupancy was one in all patches but the youngest, which resembled grassland. For these ubiquitous species the determination of correlations to patch characteristics was impossible—these include the Green-backed Camaroptera (*Camaroptera brachyuran*), Yellow-bellied Greenbul (*Chlorocichla flaviventris*), Olive Sunbird (*Cyanomitra olivacea*), and Yellow-breasted Apalis (*Apalis flavida*). For the woody plants, three species were near ubiquitous (Dune false current, *Allophylus natalensis*, Large-leaved dragon tree, *Dracaena alectrifomis*, and Quar, *Psydrax obovata*). We therefore discarded these species from the rest of the analysis.

Patch Occupancy Models

Distance from Sokhulu. For both taxa the probability of patch occupancy decreased with increasing distance from Sokhulu (Fig. 2a & 2b). Distance from Sokhulu was the most parsimonious model for eight of the 25 woody plant species (Table 1). Five of these had distance from Sokhulu as the only plausible model (Natal apricot, *Dovyalis longispina*; Septee tree, *Cordia caffra*; Zulu cherry-orange, *Teclea gerrardii*;

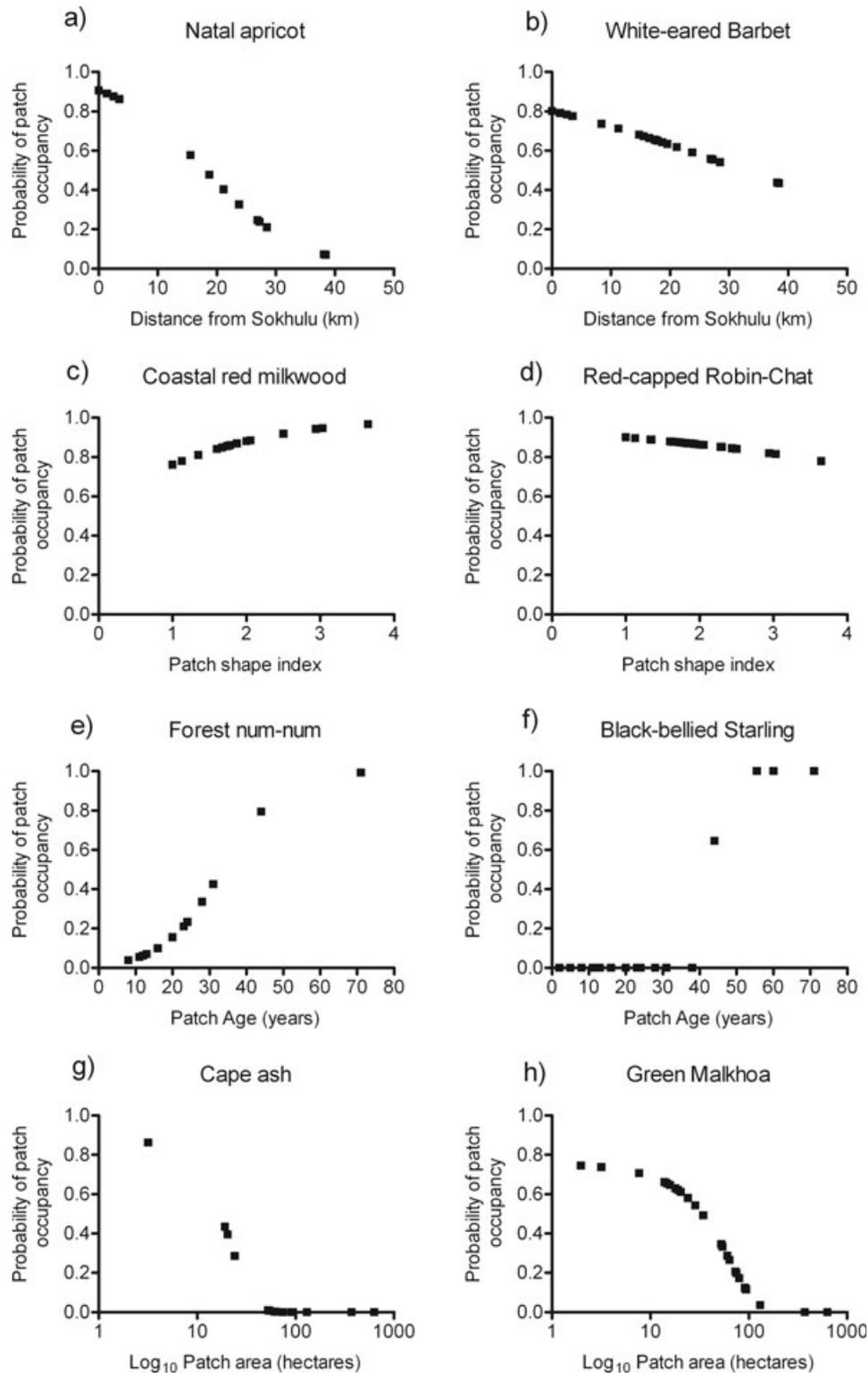


Figure 2. The probability of patch occupancy as a function of the patch characteristics distance from Sokhulu (a & b), patch shape index (c & d), patch age (e & f), and patch area (g & h). Here we show data for the trees: (a) Natal apricot (*Dovyalis longispina*), (c) Coastal red milkwood (*Mimusops caffra*), (e) Forest num-num (*Carissa bispinosa*), (g) Cape ash (*Ekebergia capensis*); and the birds: (b) White-eared Barbet (*Stactolaema leucotis*), (d) Red-capped Robin-chat (*Cossypha natalensis*), (f) Black-bellied Starling (*Lamprotornis corruscus*), and (h) Green Malkhoa (*Ceuthmochares aereus*).

Table 1. The number of species whose patch occupancy was best explained by each model, the numbers in brackets indicate the number of species that have each model as a plausible alternative.

Model	Birds	Trees
$\Psi(P_{\text{age}})$	5 (3)	11 (3)
$\Psi(P_{\text{isolation}})$	2 (3)	8 (2)
$\Psi(P_{\text{age}} + P_{\text{area}} + P_{\text{isolation}})$	0 (2)	0
$\Psi(P_{\text{age}} + P_{\text{area}} + P_{\text{shape}})$	0 (1)	0
$\Psi(P_{\text{age}} + P_{\text{area}})$	2 (0)	0
$\Psi(P_{\text{age}} + P_{\text{isolation}} + P_{\text{shape}})$	0 (1)	0
$\Psi(P_{\text{age}} + P_{\text{isolation}})$	1 (0)	0
$\Psi(P_{\text{area}} + P_{\text{isolation}} + P_{\text{shape}})$	1 (0)	0
$\Psi(P_{\text{area}} + P_{\text{shape}})$	1 (0)	0
$\Psi(P_{\text{isolation}} + P_{\text{shape}})$	1 (2)	0
$\Psi(P_{\text{shape}})$	6 (1)	3 (3)
$\Psi(P_{\text{area}})$	2 (3)	3 (4)

False ironwood, *Olea capensis*; and Coastal goldleaf, *Bridelia micrantha*). Wild honeysuckle (*Turraea floribunda*), had patch age as a plausible secondary model, but given the data and candidate models, distance from Sokhulu was 1.70 times more plausible than patch age. The Thorny elm (*Chaetachme aristata*), and the Dune soap-berry (*Deinbollia oblongifolia*), had patch area as their most plausible secondary model (the Thorny elm had high model uncertainty so had all variables as plausible alternatives). Distance from Sokhulu was 1.10 and 2.11 times more plausible for Thorny elm and Dune soap-berry, respectively (Table 2).

Two birds (out of 21) had distance from Sokhulu as their top-ranked model, the White-eared Barbet (*Stactolaema leucotis*) and the Eastern bronze-naped Pigeon (*Columba delegorguei*; Tables 1 & 2). For the Eastern bronze-naped Pigeon distance to Sokhulu was the only plausible model. The White-eared Barbet had patch shape index, distance from Sokhulu + patch shape index, and patch age as alternative models. Distance from Sokhulu was 1.08 times more plausible than the next most important variable patch shape index.

Patch Area. Patch area was the most parsimonious model for three of the 25 woody plant species (Table 1), the Cape ash (*Ekebergia capensis*), Giant pock ironwood (*Chionanthus peglerae*), and the Sea guarri (*Euclea racemosa* ssp. *sinuate*). The Sea guarri had distance from Sokhulu and patch age as plausible alternatives, but patch area was 27.10 times more plausible than distance from Sokhulu. The Giant pock ironwood tree and the Sea guarri bush had a probability of patch occupancy of 0 in any patch below 300 ha and a probability of one above 300 ha. For the Cape ash probability of patch occupancy decreased with increased patch size (Table 2; Fig. 2g).

Two of the 21 bird species had patch area as top-ranked model (Table 1). The Eastern Nicator (*Nicator gularis*) was only present in sites greater than 20 ha. In contrast, the Green Malkhoa's patch occupancy probability decreased with increasing patch area (Fig. 2h).

Patch Shape Index. Three of the 25 woody plants (Black bird-berry, *Psychotria capensis*; Coastal red milkwood, *Mimusops caffra*; and Poison olive; *Peddiea africana*) had patch shape index as their top-ranked model (Tables 1 & 2). For the Poison olive and Coastal red milkwood, as patch shape complexity increased so did the probability of patch occupancy (Fig. 2c), whereas the opposite relationship was true for the Black bird-berry. The coastal red milkwood had patch area as a plausible alternative model, but patch shape index was 10.58 times more plausible (Table 2).

For 6 out of 21 birds patch shape index was the most parsimonious model (Table 1). For the Black-backed Puffback (*Dryoscopus cubla*), Tambourine Dove (*Turtur tympanistria*), Crowned Hornbill (*Tockus alboterminatus*), and Square-tailed Drongo (*Dicrurus ludwigii*) the probability of occurrence increased with patch shape complexity. The Red-capped Robin-chat (*Cossypha natalensis*) and Tawny-flanked Prinia (*Prinia subflava*) showed the opposite relationship (as patch shape complexity increased the probability of patch occupancy decreased; Fig. 2d). The Tambourine Dove had patch area, distance from Sokhulu and patch age as plausible alternative models. Patch shape index was 1.50 times more plausible than any of the other variables for this species (Table 2).

Estimated Patch Age. For both taxa the probability of patch occupancy increased with increasing estimated patch age (Fig. 2e & 2f). Estimated patch age was the top-ranked model for 11 of 25 woody plants (Table 1). For nine of these, patch age was the only possible model considering the data and candidate model set (Table 2). These were the Acorn diospyros, *Diospyros natalensis*; False soap-berry, *Pancovia golungensis*; Forest num-num, *Carissa bispinosa*; Prickly red-berry, *Erythrococca berberidea*; Black monkey orange, *Strychnos gerrardii*; White forest spike-thorn, *Gymnosporia nemorosa*; Common coca tree, *Erythroxylum emarginatum*; and the Coast coffee, *Tricalysia sonderiana*. The Glossy forest grape (*Rhoicissus rhomboidea*) had high model uncertainty with distance from Sokhulu, patch area, and patch shape index being supported as alternative models. The Dune bride's bush (*Pavetta revoluta*) had patch shape index as an alternative. For the Glossy forest grape patch age was 1.50 times more plausible than distance from Sokhulu, whereas for the Dune bride's bush patch age was 2.40 times more plausible than patch shape index.

Five of 21 birds (Lemon Dove, *Aplopelia larvata*; Trumpeter Hornbill, *Bycanistes bucinator*; Yellow-rumped Tinkerbird, *Pogoniulus bilineatus*; Black-bellied Starling, *Lamprotonis corruscus*; and Collared Sunbird, *Hedydipna collaris*) had patch age as the only plausible model in the set (Tables 1 & 2).

Multivariate Models. Multivariate models were the top-ranked in 6 of the 21 birds and none of the woody plant species (Table 1). The Scaly-throated Honeyguide (*Indicator variegatus*), Dark-capped Bulbul (*Pycnonotus tricolor*), and the Blue-mantled crested Flycatcher (*Trochocercus cyanomelas*) all had models that included distance from Sokhulu as a variable (distance from Sokhulu + patch shape index, patch

Table 2. Results of model selection for 25 forest-associated tree species and 21 forest-associated bird species. The variables included in the model selection include patch age (1), patch area (2), distance from Sokhulu (3), and patch shape index (4).

Species	Latin name	Best model fit	Number of parameters	AICc or QAICc	w_i	Other models with substantial support (Δ AICc between 0 and 2)	Importance value			
							1	2	3	4
<i>Woody plants</i>										
Acorn diospyros	<i>Diospyros natalensis</i>	1	9	71.52	0.98		0.98	0.01	0.01	0.00
False soap-berry	<i>Pancovia golungensis</i>	1	9	67.57	0.98		0.98	0.01	0.01	0.00
Forest num-num	<i>Carissa bispinosa</i>	1	9	89.18	0.73		0.75	0.12	0.13	0.03
Prickly red-berry	<i>Erythrococca berberidea</i>	1	9	91.97	0.80		0.82	0.02	0.14	0.04
Black monkey orange	<i>Strychnos gerrardii</i>	1	9	79.24	0.62		0.63	0.09	0.19	0.10
Glossy forest grape	<i>Rhoicissus rhomboidea</i>	1	9	57.30	0.35	3,2,4	0.35	0.22	0.24	0.20
Natal ironplum	<i>Drypetes natalensis</i>	1	9	101.46	0.55		0.55	0.14	0.17	0.14
White forest spike-thorn	<i>Gymnosporia nemorosa</i>	1	9	125.94	0.72		0.72	0.06	0.05	0.16
Common coca tree	<i>Erythroxylum emarginatum</i>	1	9	98.68	0.99		1.00	0.00	0.00	0.00
Dune bride's bush	<i>Pavetta revoluta</i>	1	9	151.35	0.56	4	0.56	0.12	0.09	0.23
Coast coffee	<i>Tricalysia sonderiana</i>	1	9	175.47	0.89		0.89	0.04	0.03	0.04
Cape ash	<i>Ekebergia capensis</i>	2	9	58.11	0.74		0.05	0.74	0.03	0.18
Giant pock ironwood	<i>Chionanthus peglerae</i>	2	9	55.89	0.95		0.01	0.95	0.04	0.01
Sea guarri	<i>Euclea racemosa</i> ssp. <i>sinuate</i>	2	9	55.89	0.95	4,1	0.01	0.95	0.04	0.01
Natal apricot	<i>Dovyalis longispina</i>	3	9	111.79	0.73		0.13	0.09	0.73	0.06
Septe tree	<i>Cordia caffra</i>	3	9	85.96	0.89		0.02	0.02	0.89	0.07
Wild honeysuckle	<i>Turraea floribunda</i>	3	9	88.41	0.59	1	0.35	0.03	0.59	0.03
Zulu cherry-orange	<i>Teclea gerrardii</i>	3	9	115.64	0.83		0.05	0.06	0.83	0.06
Thorny elm	<i>Chaetachme aristata</i>	3	9	87.45	0.27	2,4,1	0.23	0.26	0.27	0.24
False ironwood	<i>Olea capensis</i>	3	9	80.27	0.90		0.02	0.02	0.90	0.06
Coastal goldleaf	<i>Bridelia micrantha</i>	3	9	108.08	0.89		0.03	0.04	0.89	0.04
Dune soap-berry	<i>Deinbollia oblongifolia</i>	3	9	164.88	0.52	2	0.15	0.25	0.52	0.09
Black bird-berry	<i>Psychotria capensis</i>	4	9	132.49	0.41		0.22	0.13	0.23	0.41
Coastal red milkwood	<i>Mimusops caffra</i>	4	9	187.44	0.78	2	0.07	0.07	0.07	0.78
Poison olive	<i>Peddiea africana</i>	4	9	112.50	0.61		0.08	0.23	0.08	0.61
<i>Birds</i>										
Lemon Dove	<i>Aplopelia larvata</i>	1	7	53.67	0.54		0.89	0.07	0.29	0.24
Trumpeter Hornbill	<i>Bycanistes bucinator</i>	1	7	86.52	0.69		0.99	0.09	0.17	0.09
Yellow-rumped Tinkerbird	<i>Pogoniulus bilineatus</i>	1	7	151.46	0.68		0.99	0.16	0.10	0.09
Black-bellied Starling	<i>Lamprotonis corruscus</i>	1	7	56.46	0.31		0.68	0.30	0.35	0.23
Collared Sunbird	<i>Hedypipna collaris</i>	1	7	144.93	0.47		0.68	0.25	0.19	0.15
Eastern Nicator	<i>Nicator gularis</i>	2	7	112.36	0.82		0.09	0.99	0.09	0.04
Green Malkhoa	<i>Ceuthmochares aereus</i>	2	7	92.74	0.56		0.22	0.76	0.14	0.14
White-eared Barbet	<i>Stactolaema leucotis</i>	3	7	104.15	0.22	4,3 + 4,2	0.26	0.14	0.52	0.48
Eastern bronze-naped Pigeon	<i>Columba delegorguei</i>	3	7	21.00	0.56		0.22	0.20	0.74	0.20
Goldentailed Woodpecker	<i>Campethera abingoni</i>	1 + 2	8	126.34	0.80		0.92	0.98	0.08	0.07
Red-fronted Tinkerbird	<i>Pogoniulus pusillus</i>	1 + 2	8	142.46	0.34	2,1 + 2 + 4	0.58	0.86	0.14	0.27
Blue-mantled crested Flycatcher	<i>Trochocercus cyanomelas</i>	1 + 3	8	86.50	0.48	1 + 2 + 3	0.93	0.43	0.88	0.10
Black-backed Puffback	<i>Dryoscopus cubla</i>	4	7	59.54	0.75		0.09	0.09	0.09	0.78
Red-capped Robin-chat	<i>Cossypha natalensis</i>	4	7	122.56	0.59		0.15	0.15	0.15	0.63
Square-tailed Drongo	<i>Dicrurus ludwigii</i>	4	7	138.11	0.99		0.00	0.00	0.00	0.99
Tambourine Dove	<i>Turtur tympanistria</i>	4	7	138.30	0.31	2,3,1	0.25	0.25	0.25	0.37
Tawny-flanked Prinia	<i>Prinia subflava</i>	4	7	164.63	0.54		0.17	0.17	0.16	0.59
Crowned Hornbill	<i>Tockus alboterminatus</i>	4	7	47.53	0.39		0.20	0.26	0.22	0.59
Brown-hooded Kingfisher	<i>Halcyon albiventris</i>	2 + 4	8	93.44	0.28	2,3,1,4	0.25	0.52	0.23	0.48
Scaly-throated Honeyguide	<i>Indicator variegatus</i>	3 + 4	8	57.83	0.45	3	0.12	0.21	0.90	0.49
Dark-capped Bulbul	<i>Pycnonotus tricolor</i>	2 + 3 + 4	9	152.25	0.37	1 + 3 + 4, 3 + 4	0.33	0.43	0.92	0.89

The most important variable for each species is in italics

area + distance to Sokhulu + patch shape index, patch age + distance from Sokhulu, respectively). Distance from Sokhulu was more important than the next most important variable shape for both the Scaly-throated Honeyguide (distance from Sokhulu was 1.81 times more plausible) and the Dark-capped Bulbul (distance from Sokhulu was 1.03 times more plausible; Table 2). Both decreased in the probability of occupancy with increasing distance from Sokhulu. For the Blue-mantled crested Flycatcher patch age was 1.06 times more important than distance to Sokhulu; Table 2). The probability of patch occupancy increased with patch age and decreased with increased distance from Sokhulu.

Where patch area was a variable in multivariable models it was the most important in three out of four cases (Table 1). Both the Goldentailed Woodpecker (*Campethera abingoni*) and Red-fronted Tinkerbird (*Pogoniulus pusillus*) had patch age + patch area as their top-ranked models, patch area was 1.10 and 1.50 times more plausible than patch age, respectively (Table 2). For both of these species as patch area increased the probability of patch occupancy decreased. For the Brown-hooded Kingfisher (*Halcyon albiventris*) patch area + patch shape index was the top-ranked model (Table 1). Patch shape index was 1.10 times more plausible than patch area. For this species, as patch shape became more complex, the probability of patch occupancy decreased.

Discussion

Previous work on the community assembly of disturbed coastal dune forest has demonstrated age-related trends in both bird and woody plant community composition (van Aarde et al. 1996; Kritzing & van Aarde 1998; Wassenaar et al. 2005). We therefore expected that patch age would be a major correlate of the probability of patch occupancy for coastal dune forest woody plants and birds. However, contrary to this expectation, patch age was not a variable in the plausible models for the majority of species assessed. Landscape structure (size, shape, and spatial arrangement of habitat patches) correlated better with the probability of patch occupancy of the remaining 15 birds and 14 woody plants. However, we found that this response was idiosyncratic and variable. Although the woody plants and birds broadly conformed to the expected differences resulting from differences in vagility (i.e. woody plants correlated better to isolation than birds), all species were not equally affected, nor did the different landscape structure parameters have the same influence.

For birds, the species-specific responses could be partly explained by their habitat affinity. Forest-edge-associated species such as the Crowned Hornbill (*Tockus alboterminatus*) and Black-backed Puffback (*Dryoscopus cubla*) were explained best by patch shape, both these species are classified as forest-edge species (Gibbon 2006) and they conformed to this classification by responding positively to edge. Surprisingly, the Square-tailed Drongo (*Dicrurus ludwigii*) a forest core species (Gibbon 2006), showed increased patch occupancy with increased edge. Habitat-edge dogma suggests that

birds which normally inhabit the forest core will be negatively affected by interactions with matrix inhabitants, through predation and nest-parasitism for example, when exposed to increased edge habitat (Brittingham & Temple 1983; Andr n & Angelstam 1988; but see Kotze & Lawes 2007). This appears not to be the case for this species. As it is an insectivore it may benefit from insect emergences that occur after rainfall along the sand roads that surround patches (M. Grainger personal observation).

Bird species with high affinity to forests are notoriously loathe to cross open areas (G mez 2003; Moore et al. 2008). However, only four birds, the White-eared Barbet (*Stactolaema leucotis*), Dark-capped Bulbul (*Pycnonotus tricolor*), Scaly-throated Honeyguide (*Indicator variegates*) and the Eastern bronze-naped Pigeon (*Columba delegorguei*), responded best to patch isolation. Species-isolation relationships may only become apparent where matrix habitat constrains movement (Wethered & Lawes 2003; Castell n & Sieving 2005; Watson et al. 2005). Our results suggest that the majority of forest birds in the study areas can cross the non-forest matrix, or make use of potential corridors such as the 200-m-wide strip of vegetation on seaward side of the mining lease. This strip however, has never been assessed as a potential movement corridor. Of the species whose patch occupancy was described best by the distance from Sokhulu the White-eared Barbet and Dark-capped Bulbul have successfully colonized the rehabilitating sites. The Eastern bronze-naped Pigeon and Scaly-throated Honeyguide have not colonized the rehabilitating sites. The Eastern bronze-naped Pigeon is a forest-associated species important in the dispersal of several large seeded trees, as well as the pioneer species Pigeon wood (*Trema orientalis*; Gibbon 2006). The further investigation of the effect of isolation on this species may therefore be important to ensure restoration success.

The nature of the matrix may also negate species–area relationships. Wethered & Lawes (2003) showed that in a high contrast landscape (forest and grassland), the species–area relationship was apparent. Whereas, in a low-contrast landscape (forest and plantation) the relationship was not, this may have been because species could gain resources from the plantation matrix and were therefore not constrained by patch area. The contrast between some of landscape elements of the mining lease area are low, forest and secondary woodland, or commercial forestry for example. This might explain why an increased patch area corresponded to an increase in patch occupancy in only two species (Eastern Nicator, *Nicator gularis* and Brown-hooded Kingfisher, *Halcyon albiventris*).

The differential responses of woody plants to measures of landscape structure for some species may also be attributed to habitat affinity. For example, woody plant species may respond positively to edge in response to abiotic variables, such as light intensity (Saunders et al. 1991). This may help explain the probability of occupancy of the Poison olive (*Peddiea africana*) which increased with increased edge. This species is typical of forest margins (Coates-Palgrave 2002). It is found in deep shade which is associated with the forest edge. Forest

edges may become dense with vegetation over time (Didham & Lawton 1999).

Woody plants may be exposed to increased seed and seedling predation at the edge of forests as seedlings or seeds are exposed to a greater number of matrix dwelling herbivores (del-Val et al. 2007). In our study area, this still requires investigation, but is a plausible mechanism for the positive correlation to patch area and patch edge demonstrated by Giant pock ironwood tree (*Chionanthus peglerae*), the Sea guarri bush (*Euclea racemosa* ssp. *sinuate*), and the Black bird-berry (*Psychotria capensis*).

The success of woody plant dispersal may be limited in tropical forests by distance (isolation effects) and dispersal vector availability (Duncan & Duncan 2000; Cordeiro & Howe 2001; Gómez 2003). Distance from Sokhulu was the top-ranked model for more woody plants in our study than any other patch variable except patch age, and all trees decreased patch occupancy with increased distance from Sokhulu. In patches closer to the unmined Sokhulu forest, these species had a higher probability of occupancy, and as the distance from this unmined area increased the probability of occupancy decreased. This may reflect a rescue effect where propagules can disperse to nearby patches and bolster the local population from extinction (Brown & Kodric-Brown 1977). As this distance increases, the probability of successful dispersal also decreases thus reducing the overall population size in isolated patches. Of course, the forest fragments that are closer to the rehabilitating patches may act as source for these species and we cannot rule out source populations other than those patches we surveyed (e.g. within the 200-m strip of vegetation along the coast).

Here we have shown a correlation between the presence of typical forest species in rehabilitating, spontaneous regenerating and remnant forest patches, and patch spatial characteristics. This means the success of a restoration program that relies upon successional processes alone may be jeopardized by the spatial characteristics of rehabilitating patches, such as their edge, and isolation from potential source. In these circumstances, managers may need to consider assisting the colonization of those species most affected by patch characteristics. It is crucial that any study of fragmentation effects also looks at the age of patches alongside traditional spatial factors (Ross et al. 2002), because both space and time may be interacting (Jacquemyn et al. 2001).

Implications for Practice

- Although time heals a number of wounds, it does not heal all of them, landscape structure is an often overriding effect on patch occupancy, implying that it may reduce the ability of species to colonize the new sites.
- Managers need to consider the landscape and its composition in restoration planning. Measures of patch edge, isolation from a mainland, and patch age were most important in explaining the distribution of some coastal dune forest bird and tree species.

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